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THE QUARTERLY REVIEW of BIOLOGY

A CRITIQUE OF KONRAD LORENZ'S THEORY OF INSTINCTIVE BEHAVIOR

BY DANIEL S. LEHRMAN

The American Museum of Natural History and Rutgers University

BEGINNING about 1931, Konrad Lorenz, with his students and collaborators (notably N. Tinbergen), has published numerous behavioral and theoretical papers on problems of instinct and innate behavior which have had a widespread influence on many groups of scientific workers (Lorenz, 1931, 1932, 1935, 1937a; Lorenz and Tinbergen, 1938; Lorenz, 1939; Tinbergen, 1939; Lorenz, 1940, 1941; Tinbergen, 1942, 1948a, 1950; Lorenz, 1950; Tinbergen, 1951). Lorenz's influence is indicated in the founding of the *Zeitschrift für Tierpsychologie* in 1937 and in its subsequent development, and also in the journal *Behaviour*, established in 1948 under the editorship of an international board headed by Tinbergen.

Lorenz's theory of instinctive and innate behavior has attracted the interest of many investigators, partly because of its diagrammatic simplicity, partly because of its extensive use of neurophysiological concepts, and partly because Lorenz deals with behavior patterns drawn from the life cycle of the animals discussed, rather than with the laboratory situations most often found in American comparative psychology. These factors go far toward accounting for the great attention paid to the theory in Europe, where most students of animal behavior are zoologists, physiologists, zoo curators or naturalists, unlike the psychologists who constitute the majority of American students of animal behavior (Schneirla, 1945).

In recent years Lorenz's theories have attracted more and more attention in the United States as well, partly because of a developing interest in animal behavior among American zoologists and ecologists, and partly through the receptive audience provided for Lorenz and his colleague, Tinbergen, by American ornithologists. The ornithologists were interested from the start, especially because a great part of the material on which Lorenz based his system came from studies of bird behavior, but the range of interest in America has widened considerably. Lorenz and his theories were recently the subject of some discussion at a conference in New York at which zoologists and comparative psychologists were both represented (Riess, 1949), and are prominently represented in the recent symposium on animal behavior of the Society of Experimental Biologists (Armstrong, 1950; Baerends, 1950; Hartley, 1950; Koehler, 1950; Lorenz, 1950; Tinbergen, 1950), and extensively used in several chapters of a recent American handbook of experimental psychology which will be a standard sourcebook for some years to come (Beach, 1951a; Miller, 1951; Nissen, 1951).

Because Lorenz's ideas have gained wide attention, and in particular because a critical discussion

of these matters should bring usefully into review Lorenz's manner of dealing with basic problems in the comparative study of behavior, a reconsideration of Lorenz's system and school seems very desirable at this time.

LORENZ'S INSTINCT THEORY

We may best represent the general characteristics of the theory under discussion in terms of a case analyzed by Lorenz and Tinbergen (1938). The many subsequent references to this case and the proffered analysis by these authors and their colleagues leave no doubt that the case and its treatment may stand as representative.

Egg-rolling in the Gray Goose

When a gray goose, sitting on its nest, sees an egg that has rolled out of the nest, it reacts in a characteristic fashion. It extends its head toward the egg and then, keeping its head and neck pointed toward the egg and its eyes fixed upon it, stands up and slowly steps forward to stand on the rim of the nest. Next the goose bends its neck downward and forward so that the egg rests against the underside of the bill. It then proceeds to roll the egg back into the nest by shoving it back between its legs, using the underside of the bill. At the same time that this movement of the head and neck is taking place in the sagittal plane, the goose performs side-to-side movements of the head which have the effect of balancing the egg against the under-side of the bill.

The instinctive act

The egg-rolling movement in the sagittal plane may be considered first, without reference to whatever side-to-side movements may occur, since these two types of movement are distinguished very sharply in the theory.

Lorenz and Tinbergen found that the goose's tendency to perform the sagittal movement can be "exhausted" by repeated elicitation, even though observations indicated that the muscles involved evidently are not themselves fatigued. The authors therefore concluded that what is exhausted is a central neural mechanism.

The form of the sagittal movement is always much the same, regardless of variations in the shape of the egg-object or irregularities in the path over which the egg is rolled. Furthermore, when the egg rolls away from its bill, the goose, instead of stopping the sagittal movement and reaching out toward the egg, frequently continues the sagittal movement to completion much as though an egg were present. The longer one waits after "exhaustion," the easier it is to reelicit the act.

In connection with certain other behavior patterns, Lorenz (1937b) has noted that, after long resting intervals, the animal may perform a complete act without any external stimulus. This performance "in a vacuum" is regarded by Lorenz as the extreme case of the lowering of the threshold of elicitation after long non-exercise of the act. He calls it "Leerlaufreaktion," or "going off in a vacuum" [translated by Tinbergen (1942) as "vacuum activities"].

The sagittal movement thus has the following characteristics: (1) it displays a reaction-specific exhaustibility; (2) although released by stimuli coming from the egg, once released it remains constant in form regardless of variations in stimulation from the environment and even of the presence or absence of the original releasing stimulus; and (3) the threshold for elicitation falls continuously during non-exercise of the act.

The movement in the sagittal plane, distinguished from lateral deviations, is a typical "instinctive act" (Erbkoordination) in Lorenz's system. This "instinctive act," of course, is only a part of the total behavior pattern of egg-rolling. However, Lorenz maintains that every "instinctive" behavior pattern has as its focus such an "instinctive act" or "consummatory act" (Craig, 1918), the performance of which serves as goal for much of the rest of the pattern.

To Lorenz, *the* instinctive act is a rigidly stereotyped innate movement or movement pattern, based on the activity of a specific coordinating center in the central nervous system. In this coordinating center, there is a continuous accumulation of excitation or energy specific for the act. When the animal comes into the appropriate external situation for the performance of the act, stimuli provided by that situation release the energy, the instinctive act is performed, and some or all of the excitation is used up. The center specific for the act thus is able to coordinate the instinctive act completely independently of the receptors, so that once the act is released (i.e., elicited) its performance occurs in complete form, coordinated by impulses from the center and without any chain-reflex character. The function of the stimulus is to release or elicit the act. Once released, the act no longer depends for its form on

anything outside the central nervous system. When the animal happens *not* to be in the appropriate stimulus-situation, this reaction-specific energy is presumed to be accumulated, or dammed up. Also, the greater the amount of reaction-specific energy which has accumulated, the more easily may the act be elicited and the more complete will be its form when elicited.

This picture is regarded by Lorenz as a representation of the neurophysiological basis of the above-described functional characteristics of the instinctive act. In particular, accumulation of energy in a neural center capable of determining the form and order of performance of the various movements of the act, independently of the receptors (except for a trigger-like elicitation), is postulated to explain the reaction-specific exhaustibility (using up of the specific energy), the presumed independence of the form of the act from concurrent external stimulation (reaction-specificity of the energy), and the lowering of the threshold during a non-exercise interval (i.e., when an accumulation of reaction-specific excitation is presumed to occur).

The innate releasing mechanism

If energy specific for the instinctive act can accumulate continuously in the neural center specific for that act, why is the act not continuously performed? Tinbergen (1948a) concludes that each coordinating center is normally held under inhibition by another center which functions to block impulses from the coordinating center, save under specific conditions of external stimulation. This postulated inhibiting center is called the "innate releasing mechanism." The effect of an external stimulus which elicits an instinctive act is to release the instinctive center from this inhibition.

For example, the sagittal component of the goose's egg-rolling movement is not performed continuously, even though energy specific for it is being produced continuously in the central nervous system. The movement is only performed in a particular stimulus-situation: i.e., when a smooth-outlined hard object is present near the nest. (In non-experimental situations, such an object in such a place will almost always be an egg that has rolled out of the nest.) This combination of stimuli, which is considered capable of releasing the particular instinctive act from the inhibition under which it is held by the innate releasing mechanism, is called the "innate releasing pattern." According to Lorenz and Tinbergen (1938), "The innate releasing pattern . . . [is] . . . the innately-determined readiness of an animal to respond to a particular combination of external stimuli with a particular behavior. It thus consists of an innate receptoral correlate of a combination of stimuli which, despite its relative simplicity, characterizes a certain biologically-significant situation sufficiently uniquely so that the animal will not normally perform the appropriate reaction except in that situation."

The view, then, is that the innate releasing mechanism holds the instinctive act under inhibition until there appears a specific innate releasing pattern of stimuli capable of switching off the inhibition and "triggering" an outflow of impulses from the instinctive center to the peripheral effectors.

Also, the higher the level reached by the accumulation of reaction-specific energy in the center, the more difficult is presumed to be any inhibition of the act by the releasing mechanism. Consequently, the less completely does any stimulus-combination need to fit the innate releasing pattern as a whole to elicit the act. This explanation is offered by Lorenz for the fact that the instinctive act is easier to elicit, the more time has elapsed since it was last performed. The Leerlaufreaktion thus is a breaking of reaction-specific energy through the inhibiting barrier, when such energy reaches a very high level.

The taxis

Side-to-side movements of the head, by which the goose keeps the egg balanced against the underside of the bill, unlike the sagittal movement, lack the character of centrally-preformed movement patterns. The side-to-side movements are believed to be elicited independently by contact stimulation of the underside of the bill by the egg being rolled. Whenever the egg rolls off center, a bill movement toward the side of the deviation restores the egg to the path. If the egg happens to roll free so that the bird may continue the sagittal movement without any egg, there are no accompanying side-to-side movements. When the bird is permitted to roll a cylinder, there are usually no side-to-side movements, since a cylinder is unlikely to roll from side to side in its path.

Thus the side-to-side movement is not only *elicited* by external stimuli like the sagittal movement, but is also continuously *oriented* with respect

to external stimuli while being performed. In this respect lateral deviations differ fundamentally from the instinctive act, the form of which is determined centrally so that the external stimulus acts as a trigger only.

Movements like the side-to-side movements, which are continuously oriented to stimuli during their performance, are called by Lorenz orienting movements, or *taxes*. A taxis may occur simultaneously with an instinctive act (as in the case of the goose's egg-rolling), or may occur interspersed with instincts in a behavior-chain.

The stimuli releasing the act (innate releasing pattern for the instinctive act), according to Tinbergen (Tinbergen and Kuenen, 1939; Tinbergen, 1942) are not necessarily the same as those guiding it (i.e., the innate receptor pattern for the taxis). In the case of egg-rolling, for example, the instinctive act is released by a combination of visual stimuli and tactual stimuli related to the hardness of the egg, as felt by the tip of the bill in tapping. The (side-to-side) taxis, on the other hand, is released by tactual stimuli on the underside of the bill.

Appetitive behavior

The first part of the goose's reaction to the egg outside the nest is a stretching of the neck forward and downward, toward the egg. This act, according to Lorenz, has a different character from the instinctive act itself. It serves the purpose of getting the animal into the particular situation in which a specific instinctive act can be released. The act thus is truly goal-directed, according to Lorenz, who terms it "appetitive behavior" (Appetenzverhalten). He regards *all* goal-directed behavior as appetitive, in the sense that such acts are directed toward getting the animal into a situation in which some instinctive act can be released. For him, appetitive behavior can be of enormous complexity, involving instincts, taxes, and learned behavior of various kinds. Such behavior normally occurs when the level of excitation in the central nervous system for any instinctive act becomes high enough. This causes the animal to become restless and active. What specific kind of activity may occur depends on the kind of animal, and on which instinct is the source of the appetitive restlessness. For example, a rat set into activity by a high level of energy specific for the instinctive act of eating (i.e., he wants to eat) may turn toward a corner of the cage, walk toward it, pick up a piece of food in its paws, bite at it, and chew it. Now, the whole sequence of behavior in this hypothetical example would be regarded by Lorenz as appetitive to the instinctive act of chewing. For him, turning toward the corner is a taxis, the walking is an instinctive act, picking up the food might be an instinct, turning the head toward the food held in the paws is a taxis, and the chewing an instinct. Which corner the rat turns toward depends on his past experience—the taxis is thus partly learned. The turning of the head toward the food in the paws, however, might be innate. [Tinbergen (1942) points out that some taxes may be learned, others innate. According to Lorenz's system, however, all instinctive acts (as distinct from taxes) are innate.]

For Lorenz, the whole complex of behavior in this example, involving instincts and taxes, learned and innate elements, has at its core the act of chewing, and is motivated by the excitation set up by the neural center for chewing. The appetitive behavior continues until the instinctive act is performed, and the specific energy is thus used up. It is important to note that according to Lorenz the goal of the appetitive behavior is the *performance* of the act, not its biological result. That is to say, in our hypothetical case, the need of which the appetitive restlessness is an expression is reduced not by the introduction of food into the stomach, but by the act of chewing. This is shown more clearly in the case of instinctive acts like courtship displays of birds, which form the goal of appetitive behavior (moving toward the female, orienting to the female, etc.) and which according to Lorenz are subject to Leerlaufreaktionen even though they do not (like chewing and swallowing) result in the satisfaction of an *apparent* peripheral tissue need.

PROBLEMS RAISED BY INSTINCT THEORIES

Even this brief summary brings to light several questions which ought to be critically examined with reference to the theory. These are questions, furthermore, which apply to instinct theories in general. Among them are: (1) the problem of "innateness" and the maturation of behavior; (2) the problem of levels of organization in an organism; (3) the nature of evolutionary levels of behavioral organization, and the use of the comparative method in studying them; and (4) the manner in which physiological concepts may be properly used in behavior analysis. There follows

an evaluation of Lorenz's theory in terms of these general problems.

"Innateness" of behavior

The problem

Lorenz and Tinbergen consistently speak of behavior as being "innate" or "inherited" as though these words surely referred to a definable, definite, and delimited category of behavior. It would be impossible to overestimate the heuristic value which they imply for the concepts "innate" and "not-innate." Perhaps the most effective way to throw light on the "instinct" problem is to consider carefully just what it means to say that a mode of behavior is innate, and how much insight this kind of statement gives into the origin and nature of the behavior.

Tinbergen (1942), closely following Lorenz, speaks of instinctive acts as "highly stereotyped, coordinated movements, the neuromotor apparatus of which belongs, in its complete form, to the hereditary constitution of the animal." Lorenz (1939) speaks of characteristics of behavior which are "hereditary, individually fixed, and thus open to evolutionary analysis." Lorenz (1935) also refers to perceptual patterns ("releasers") which are presumed to be innate because they elicit "instinctive" behavior the *first time* they are presented to the animal. He also refers to those motor patterns as innate which occur for the first time when the proper stimuli are presented. Lorenz's student Grohmann (1938), as well as Tinbergen and Kuenen (1939), speak of behavior as being innately determined because it matures instead of developing through learning.

It is thus apparent that Lorenz and Tinbergen, by "innate" behavior, mean behavior which is hereditarily determined, which is part of the original constitution of the animal, which arises quite independently of the animal's experience and environment, and which is distinct from acquired or learned behavior.

It is also apparent, explicitly or implicitly, that Lorenz and Tinbergen regard as the major *criteria* of innateness that: (1) the behavior be stereotyped and constant in form; (2) it be characteristic of the species; (3) it appear in animals which have been raised in isolation from others; and (4) it develop fully-formed in animals which have been prevented from practicing it.

Undoubtedly, there are behavior patterns which meet these criteria. Even so, this does not necessarily imply that Lorenz's *interpretation* of these behavior patterns as "innate" offers genuine aid to a scientific understanding of their origin and of the mechanisms underlying them.

In order to examine the soundness of the concept of "innateness" in the analysis of behavior, it will be instructive to start with a consideration of one or two behavior patterns which have already been analyzed to some extent.

Pecking in the chick

Domestic chicks characteristically begin to peck at objects, including food grains, soon after hatching (Shepard and Breed, 1913; Bird, 1925; Cruze, 1935; and others). The pecking behavior consists of at least three highly stereotyped components: head lunging, bill opening and closing, and swallowing. They are ordinarily coordinated into a single resultant act of lunging at the grain while opening the bill, followed by swallowing when the grain is picked up. This coordination is present to some extent soon after hatching, and improves later (even, to a slight extent, if the chick is prevented from practicing).

This pecking is stereotyped, characteristic of the species, appears in isolated chicks, is present at the time of hatching, and shows some improvement in the absence of specific practice. Obviously, it qualifies as an "innate" behavior, in the sense used by Lorenz and Tinbergen.

Kuo (1932a-d) has studied the embryonic development of the chick in a way which throws considerable light on the origin of this "innate" behavior. As early as three days of embryonic age, the neck is passively bent when the heartbeat causes the head (which rests on the thorax) to rise and fall. The head is stimulated tactually by the yolk sac, which is moved mechanically by amnion contractions synchronized with the heartbeats which cause head movement. Beginning about one day later, the head first bends *actively* in response to tactual stimulation. At about this time, too, the bill begins to open and close when the bird nods—according to Kuo, apparently through nervous excitation furnished by the head movements through irradiation in the still-incomplete nervous system. Bill-opening and closing become independent of head-activity only somewhat later. After about 8 or 9 days, fluid forced into the throat by the bill and head movements causes swallowing. On the twelfth day, bill-opening always follows head-movement.

In the light of Kuo's studies the "innateness" of the chick's pecking takes on a different character from that suggested by the concept of a unitary, innate item of behavior. Kuo's observations strongly suggest several interpretations of the *development* of pecking (which, of course, are subject to further clarification). For example, the head-lunge arises from the passive head-bending which occurs contiguously with tactual stimulation of the head while the nervous control of the muscles is being established. By the time of hatching, head-lunging in response to tactual stimulation is very well established (in fact, it plays a major role in the hatching process).

The genesis of head-lunging to visual stimulation in the chick has not been analyzed. In *Amblystoma*, however, Coghill (1929) has shown that a closely analogous shift from tactual to visual control is a consequence of the establishment of certain anatomical relationships between the optic nerve and the brain region which earlier mediated the lunging response to tactual stimulation, so that visual stimuli come to elicit responses established during a period of purely tactual sensitivity. If a similar situation obtains in the chick, we would be dealing with a case of intersensory equivalence, in which visual stimuli, because of the anatomical relationships between the visual and tactual regions of the brain, became equivalent to tactual stimuli, which in turn became effective through an already analyzed process of development, which involved conditioning at a very early age (Maier and Schneirla, 1935).

The originally diffuse connection between head-lunge and bill-opening appears to be strengthened by the repeated elicitation of lunging and billing by tactual stimulation by the yolk sac. The repeated elicitation of swallowing by the pressure of amniotic fluid following bill-opening probably is important in the establishment of the post-hatching integration of bill-opening and swallowing.

Maternal behavior in the rat

Another example of behavior appearing to fulfil the criteria of "innateness" may be found in the maternal behavior of the rat.

Pregnant female rats build nests by piling up strips of paper or other material. Mother rats will "retrieve" their pups to the nest by picking them up in the mouth and carrying them back to the nest. Nest-building and retrieving both occur in all normal rats; they occur in rats which have been raised in isolation; and they occur with no evidence of previous practice, since both are performed well by primiparous rats (retrieving may take place for the first time only a few minutes after the birth of the first litter of a rat raised in isolation). Both behavior patterns therefore appear to satisfy the criteria of "innateness" (Wiesner and Sheard, 1933).

Riess (pers. com.), however, raised rats in isolation, at the same time preventing them from ever manipulating or carrying any objects. The floor of the living cage was of netting so that feces dropped down out of reach. All food was powdered, so that the rats never carried food pellets. When mature, these rats were placed in regular breeding cages. They bred, but did *not* build normal nests or retrieve their young normally. They scattered nesting material all over the floor of the cage, and similarly moved the young from place to place without collecting them at a nest-place.

Female rats do a great deal of licking of their own genitalia, particularly during pregnancy (Wiesner and Sheard, 1933). This increased licking during pregnancy has several probable bases, the relative importance of which is not yet known. The increased need of the pregnant rat for potassium salts (Heppel and Schmidt, 1938) probably accounts in part for the increased licking of the salty body fluids as does the increased irritability of the genital organs themselves. Birch (pers. com.) has suggested that this genital licking may play an important role in the development of licking and retrieving of the young. He is raising female rats fitted from an early age with collars made of rubber discs, so worn that the rat is effectively prevented from licking its genitalia. Present indications, based on limited data, are that rats so raised eat a high percentage of their young, that the young in the nest may be found under any part of the female instead of concentrated posteriorly as with normal mother rats, and that retrieving does not occur.

These considerations raise some questions concerning nativistic interpretations of nest-building and retrieving in the rat, and concerning the meaning of the criteria of "innateness." To begin with, it is apparent that practice in carrying food pellets is partly equivalent, for the development of nest-building and retrieving, to practice in carrying nesting-material, and in carrying the young. Kinder (1927) has shown that nest-building ac-

tivity is inversely correlated with environmental temperature, and that it can be stopped by raising the temperature sufficiently. This finding, together with Riess's experiment, suggests that the nest-building activity arises from ordinary food (and other object) manipulation and collection under conditions where the accumulation of certain types of manipulated material leads to immediate satisfaction of one of the animal's needs (warmth). The fact that the rat is generally more active at lower temperatures (Browman, 1943; Morgan, 1947) also contributes to the probability that nest-building activity will develop. In addition, the rat normally tends to stay close to the walls of its cage, and thus to spend much time in corners. This facilitates the collection of nesting material into one corner of the cage, and the later retrieving of the young to that corner. Patrick and Laughlin (1934) have shown that rats raised in an environment without opaque walls do not develop this "universal" tendency of rats to walk close to the wall. Birch's experiment suggests that the rat's experience in licking its own genitalia helps to establish retrieving as a response to the young, as does its experience in carrying food and nesting material.

Maturation-vs.-learning, or development?

The isolation experiment

These studies suggest some second thoughts on the nature of the "isolation experiment." It is obvious that by the criteria used by Lorenz and other instinct theorists, pecking in the chick and nest-building and retrieving in the rat are not "learned" behavior. They fulfil all criteria of "innateness," i.e., of behavior which develops without opportunity for practice or imitation. Yet, in each case, analysis of the developmental process involved shows that the behavior patterns concerned are not unitary, autonomously developing things, but rather that they emerge ontogenetically in complex ways from the previously developed organization of the organism in a given setting.

What, then is wrong with the implication of the "isolation experiment," that behavior developed in isolation may be considered "innate" if the animal did not practice it specifically?

Lorenz repeatedly refers to behavior as being innate because it is displayed by animals raised in isolation. The raising of rats in isolation, and their subsequent testing for nesting behavior, is typical of isolation experiments. The development of the chick inside the egg might be regarded as the ideal isolation experiment.

It must be realized that an animal raised in isolation from fellow-members of his species *is not necessarily isolated from the effect of processes and events which contribute to the development of any particular behavior pattern*. The important question is not "Is the animal isolated?" but "*From what* is the animal isolated?" The isolation experiment, if the conditions are well analyzed, provides at best a negative indication that certain specified environmental factors probably are not directly involved in the genesis of a particular behavior. However, the isolation experiment by its very nature does not give a positive indication that behavior is "innate" or indeed any information at all about what the process of development of the behavior really consisted of. The example of the nest-building and retrieving by rats which are isolated from other rats but not from their food pellets or from their own genitalia illustrates the danger of assuming "innateness" merely because a *particular* hypothesis about learning seems to be disproved. This is what is consistently done by Tinbergen, as, for example, when he says (1942) of certain behavior patterns of the three-spined stickleback: "The releasing mechanisms of these reactions are all innate. A male that was reared in isolation . . . was tested with models before it had ever seen another stickleback. The . . . [stimuli] . . . had the same releaser functions as in the experiments with normal males." Such isolation is by no means a final or complete control on possible effects from experience. For example, is the "isolated" fish uninfluenced by its own reflection from a water film or glass wall? Is the animal's experience with human handlers, food objects, etc., really irrelevant?

Similarly, Howells and Vine (1940) have reported that chicks raised in mixed flocks of two varieties, when tested in a Y-maze, learn to go to chicks of their own variety more readily than to those of the other variety. They concluded that the "learning is accelerated or retarded . . . because of the directive influence of innate factors." In this case, Schneirla (1946) suggests that the effect of the chick's experience with its own chirping during feeding has not been adequately considered as a source of differential learning previous to the experiment. This criticism may also be made of a similar study by Schoolland (1942) using chicks and ducklings.

Even more fundamental is the question of what

is meant by "maturation." We may ask whether experiments based on the assumption of an absolute dichotomy between maturation and learning ever really tell us *what* is maturing, or how it is maturing? When the question is examined in terms of *developmental* processes and relationships, rather than in terms of preconceived categories, the maturation-versus-learning formulation of the problem is more or less dissipated. For example, in the rat nest-building probably does not mature autonomously—and it is *not* learned. It is not "nest-building" which is learned. Nest-building develops in certain situations through a developmental process in which at each stage there is an identifiable interaction between the environment and organic processes, and within the organism; this interaction is based on the preceding stage of development and gives rise to the succeeding stage. These interactions are present from the earliest (zygote) stage. Learning may emerge as a factor in the animal's behavior even at early embryonic stages, as pointed out by Carmichael (1936).

Pecking in the chick is also an emergent—an integration of head, bill, and throat components, each of which has its own developmental history. This integration is already partially established by the time of hatching, providing a clear example of "innate" behavior in which the statement "It is innate" adds nothing to an understanding of the developmental process involved. The statement that "pecking" is innate, or that it "matures," leads us *away* from any attempt to analyze its specific origins. The assumption that pecking grows *as* a pecking *pattern* discourages examination of the embryological processes leading to pecking. The elements out of whose interaction pecking emerges are not originally a unitary pattern; they *become* related as a consequence of their positions in the organization of the embryonic chick. The understanding provided by Kuo's observations owes nothing to the "maturation-versus-learning" formulation.

Observations such as these suggest many new problems the relevance of which is not apparent when the patterns are nativistically interpreted. For example, what is the nature of the rat's temperature-sensitivity which enables its nest-building to vary with temperature? How does the animal develop its ability to handle food in specific ways? What are the physiological conditions which promote licking of the genitalia, etc.? We want to know much more about the course of establishment of the connections between the chick's head-lunge and bill-opening, and between bill-opening and swallowing. This does *not* mean that we expect to establish which of the components is learned and which matured, or "how much" each is learned and how much matured. The effects of learning and of structural factors differ, not only from component to component of the pattern, but also from developmental stage to developmental stage. What is required is a continuation of the careful analysis of the characteristics of each developmental stage, and of the transition from each stage to the next.

Our scepticism regarding the heuristic value of the concept of "maturation" should not be interpreted as ignorance or denial of the fact that the physical growth of varied structures plays an important role in the development of most of the kinds of behavior patterns under discussion in the present paper. Our objection is to the *interpretation* of the role of this growth that is implied in the notion that the *behavior* (or a *specific* physiological substrate for it) is "maturing." For example, the post-hatching improvement in pecking ability of chicks is very probably due in part to an increase in strength of the leg muscles and to an increase in balance and stability of the standing chick, which results partly from this strengthening of the legs and partly from the development of equilibrium responses (Cruze, 1935). Now, isolation or prevention-of-practice experiments would lead to the conclusion that this part of the improvement was due to "maturation." Of course it is partly due to growth processes, *but what is growing is not pecking ability*, just as, when the skin temperature receptors of the rat develop, what is growing is not nest-building activity, *or anything isomorphic with it*. The use of the categories "maturation-vs.-learning" as explanatory aids usually gives a false impression of unity and directedness in the growth of the behavior pattern, when actually the behavior pattern is not primarily unitary, nor does development proceed in a straight line toward the completion of the pattern.

It is apparent that the use of the concept of "maturation" by Lorenz and Tinbergen as well as by many other workers is not, as it at first appears, a reference to a process of development but rather to ignoring the process of development. To say of a behavior that it develops by maturation is tantamount to saying that the obvious forms of learning do not influence it, and that we therefore do not

consider it necessary to investigate its ontogeny further.

Heredity-vs.-environment, or development?

Much the same kind of problem arises when we consider the question of what is "inherited." It is characteristic of Lorenz, as of instinct theorists in general, that "instinctive acts" are regarded by him as "inherited." Furthermore, inherited behavior is regarded as sharply distinct from behavior acquired through "experience." Lorenz (1937a) refers to behavior which develops "entirely independent of all experience."

It has become customary, in recent discussions of the "heredity-environment" problem, to state that the "hereditary" and "environmental" contributions are both essential to the development of the organism; that the organism could not develop in the absence of either; and that the dichotomy is more or less artificial. [This formulation, however, frequently serves as an introduction to elaborate attempts to evaluate what part, or even what percentage, of behavior is genetically determined and what part acquired (Howells, 1945; Beach, 1947a; Carmichael, 1947; Stone, 1947).] Lorenz does not make even this much of a concession to the necessity of developmental analysis. He simply states that some behavior patterns are "inherited," others "acquired by individual experience." I do not know of any statement of either Lorenz or Tinbergen which would allow the reader to conclude that they have any doubts about the correctness of referring to behavior as simply "inherited" or "genically controlled."

Now, what exactly is meant by the statement that a behavior pattern is "inherited" or "genically controlled"? Lorenz undoubtedly does not think that the zygote contains the instinctive act in miniature, or that the gene is the equivalent of an entelechy which purposefully and continuously tries to push the organisms's development in a particular direction. Yet one or both of these preformistic assumptions, or their equivalents, must underlie the notion that some behavior patterns are "inherited" as such.

The "instinct" is obviously not present in the zygote. Just as obviously, it is present in the behavior of the animal after the appropriate age. The problem for the investigator who wishes to make a causal analysis of behavior is: How did this behavior come about? The use of "explanatory" categories such as "innate" and "genically fixed" obscures the necessity of investigating developmental *processes* in order to gain insight into the actual mechanisms of behavior and their interrelations. The problem of development is the problem of the development of new structures and activity patterns from the resolution of the interaction of *existing* structures and patterns, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the *current* stage and between the *current* stage and the environment. The interaction out of which the organism develops is *not* one, as is so often said, between heredity and environment. It is between *organism* and environment! And the organism is different at each different stage of its development.

Modern physiological and biochemical genetics is fast destroying the conception of a straight-line relationship between gene and somatic characteristic. For example, certain strains of mice contain a mutant gene called "dwarf." Mice homozygous for "dwarf" are smaller than normal mice. It has been shown (Smith and MacDowell, 1930; Keeler, 1931) that the cause of this dwarfism is a deficiency of pituitary growth hormone secretion. Now what are we to regard as "inherited"? Shall we change the name of the mutation from "dwarf" to "pituitary dysfunction" and say that dwarfism is not inherited as such—that what is inherited is a hypoactive pituitary gland? This would merely push the problem back to an earlier stage of development. We now have a better understanding of the origin of the dwarfism than we did when we could only say it is "genically determined." However, the pituitary function developed, in turn, in the context of the mouse as it was when the gland was developing. The problem is: What was that context and how did the gland develop out of it?

What, then, is inherited? From a somewhat similar argument, Jennings (1930) and Chein (1936) concluded that only the zygote is inherited, or that heredity is only a stage of development. There is no point here in involving ourselves in tautological arguments over the definition of heredity. It is clear, however, that to say a behavior pattern is "inherited" throws no light on its *development* except for the purely negative implication that *certain types* of learning are not directly involved. Dwarfism in the mouse, nest-building in the rat, pecking in the chick, and the "zig-zag

dance" of the stickleback's courtship (Tinbergen, 1942) are all "inherited" in the sense and by the criteria used by Lorenz. But they are not by any means phenomena of a common type, nor do they arise through the same kinds of developmental processes. To lump them together under the rubric of "inherited" or "innate" characteristics serves to block the investigation of their origin just at the point where it should leap forward in meaningfulness. [Anastasi and Foley (1948), considering data from the field of human differential psychology, have been led to somewhat the same formulation of the "heredity-environment" problem as is presented here.]

Taxonomy and Ontogeny

Lorenz (1939) has very ably pointed out the potential importance of behavior elements as taxonomic characteristics. He has stressed the fact that evolutionary relationships are expressed just as clearly (in many cases more clearly) by similarities and differences in behavior as by the more commonly used physical characteristics. Lorenz himself has made a taxonomic analysis of a family of birds in these terms (Lorenz, 1941), and others have been made by investigators influenced by him (Delacour and Mayr, 1945; Adriaanse, 1947; Baerends and Baerends-van Roon, 1950). This type of analysis derives from earlier work on the taxonomic relations of behavior patterns by Whitman (1898, 1919), Heinroth (1910, 1930), Petrunkevitsch (1926), and others.

Lorenz's brilliant approach to the taxonomic analysis of behavior characteristics has had wide influence since it provides a very stimulating framework in which to study species differences and the specific characteristics of behavior. However, it does not necessarily follow from the fact that behavior patterns are species-specific that they are "innate" as patterns. We may emphasize again that the systematic stability of a characteristic does not indicate anything about its mode of development. The fact that a characteristic is a good taxonomic character does not mean that it developed autonomously. The shape of the skull bones in rodents, which is a good taxonomic character (Romer, 1945), depends in part upon the presence of attached muscles (Washburn, 1947). We cannot conclude that because a behavior pattern is taxonomically stable it must develop in a unitary, independent way.

In addition it would be well to keep in mind that the species-characteristic nature of many behavior patterns may result partly from the fact that all members of the species grow in the same environment. Smith and Guthrie (1921) call such behavior elements "coenotropes." Further, it is not at all necessary that these common features of the environment be those which seem a priori to be relevant to the behavior pattern under study. Lorenz's frequent assumption (e.g., 1935) that the effectiveness of a given stimulus on first presentation demonstrates an innate sensory mechanism specific for that stimulus is not based on analysis of the origin of the stimulus-effectiveness, but merely on the fact that Lorenz has eliminated the major alternative *he* sees to the nativistic explanation.

Thorpe and Jones (1937) have shown that the apparently innate choice of the larvae of the flour moth by the ichneumon fly *Nemerites* as an object in which to deposit its eggs is actually a consequence of the fact that the fly larva was *fed* on the larvae of the flour moth while it was developing. By raising *Nemerites* larvae upon the larvae of *other* kinds of moth Thorpe and Jones caused them, when adult, to choose preponderantly these other moths on which to lay their eggs. The choice of flour-moth larvae for oviposition is quite characteristic of *Nemerites* in nature. In view of Thorpe and Jones' work, it would obviously be improper to conclude from this fact that the choice is based on innately-determined stimuli. Yet, before their paper was published, the species-specific character of the behavior would have been just as impressive evidence for "innateness" as species-specificity *ever* is.

Taxonomic analysis, while very important, is not a substitute for concrete analysis of the ontogeny of the given behavior, as a source of information about its origin and organization.

Levels of Organization

Levels of "Innateness"

Animals at different evolutionary levels show characteristic differences in the extent and manner of learning. In addition, within the same animal's behavior different activities may be more or less susceptible to the influence of learning, and may be affected in different ways by learning (Schneirla, 1948, 1949a).

Lorenz explains these facts in terms of the richness of the animal's instinctive equipment. As described above, his conception is that instinctive

behavior is sharply different from all behavior leading up to the performance of the instinct. This "appetitive" behavior is conceived of as the sole evolutionary source of all learned and intelligent behavior. Thus he says:

> "... appetitive behavior, as the sole root of all "variable" behavior, not only is physiologically something fundamentally different from the automatism of instinctive behavior, but ... the two different processes appear as "substitutes" (*vikariierend*) for each other, in that the higher (phylogenetic) development of the one makes the other superfluous and stops its development. The reaching of a higher psychic performance goes hand-in-hand with a reduction of the automatisms that take part in the action, leaving a behavior pattern with the same function as the one originally existing" (Lorenz, 1937a).

Again:

> "It is a peculiarity of many behavior patterns of higher animals, that *innate instinctive elements and individually-acquired elements immediately follow each other*, within a functionally unitary chain of acts ... I have characterized this phenomenon as instinct-training interlacement. Similar interlacements occur between instinctive acts and intelligent or insightful behavior. ... The essence of such an interlacement is that, within a chain of innate instinctive acts there is a definite point, which point is innately determined, where a learned act is inserted. This learned act must be acquired by each individual in the course of its ontogenetic development. In such a case, the chain of innate acts has a *gap*, in which, instead of an instinctive act, there is a *'capacity to acquire'* " (Lorenz, 1937a). [All emphases are Lorenz's.]

It is apparent that Lorenz regards differences in the extent to which learning occurs as representing differences in the size of the gaps in the chain of innate behavior. He considers any given "component" of behavior as "innate" or not "innate." This is entirely consistent with his virtual identification of "innate" with "autonomously developing."

However, we have already tried to make it clear that behavior patterns classified as "innate" by *any* criterion do not all fall into the same category with respect to embryonic origin, developmental history, or level of organization. Lorenz notes that more or fewer of the components of behavior may be "innate." But nowhere does he recognize that *one* component may be more or less "innate" or "innate" in one or another *manner*. We may call attention to an important difference between the pecking of the chick and the nest-building of the rat, both behavior patterns which develop without specific practice of the patterns: a major part of the learning which appears to be antecedent to the emergence of pecking in the chick occurs before hatching, while much of the learning which is antecedent to the emergence of nest-building in the rat occurs after birth.

Shall we call those behavior patterns "innate" which develop before birth and not those which develop after? This would be fruitless in view of the demonstrated existence of prenatal conditioning (Ray, 1932; Gos, 1933; Spelt, 1948; Hunt, 1949), and unsatisfactory in view of the problem of the so-called postnatal "maturation" of various "innate" behavior patterns (Grohmann, 1938). But we must recognize that different behavior patterns may involve learning at different ontogenetic stages to different extents, and in different ways. For example, much less of the behavior of the rat is *directly* a consequence of the specific characteristics of its structure than in the case of the earthworm (Maier and Schneirla, 1935). The involvement of learning in the development of the rat's behavior is different from and occurs at different developmental stages from that of the chick. Further, some responses of the rat (such as licking of a painful spot) are very much less subject to change by learning than others, such as care of young (Sperry, 1945; Uyldert, 1946). These are not differences in the *number* of behavioral elements which are "innate," but rather in the *way* in which the structures are involved in the development of behavior at different evolutionary levels and for different behavior patterns.

Lorenz does not fully utilize the idea of levels of organization of behavior, apparently because his concept of "innateness" is not the result of analysis of the development of behavior; it is in part the result of a preconception that "innate" and "not-innate" are the two categories into which behavior logically falls. Consequently Lorenz and his school have classified behavior as "innate" and "not-innate" on the basis of criteria which when carefully examined appear to be arbitrary. Their category of "innate" therefore includes very different kinds of behavior, which involve learning in many different ways. Lorenz's concept of "innate" behavior represents a lumping-together of many different kinds and levels of behavior on the basis of an essentially phenotypic classification, and the imposition of preconcieved categories upon that classification.

Evolutionary Levels

Since Lorenz does not discuss the existence of qualitative differences with respect to modes of

development within his category of "innate" behavior it is not surprising that his conception of the evolution of behavior lacks any notion of qualitative change. Lorenz maintains at all levels a sharp distinction between "instinctive acts" and "appetitive behavior" (which includes all oriented, goal-directed, and variable types of behavior at all levels). He says:

> "If we consider the unbroken series of forms of corresponding modes of behavior, which extends in a smooth progression from protozoa to man, we must determine that we cannot distinguish between taxis, on the one hand, and, on the other, behavior guided by the simplest intelligence (Einsicht). We cannot here distinguish between taxis and, in the case of our frog, an intelligence which might (anthropomorphically speaking) be limited to the knowledge: 'There sits the fly'" (Lorenz, 1937a).

This is restated in a later paper (Lorenz, 1939): "No sharp line can be drawn between the simplest orienting-reaction and the highest 'insightful' behavior."

It might be pointed out that whether we can distinguish various levels of behavioral organization depends in part on our assiduity in *attempting* to distinguish them. Preconceptions about the number and kind of categories into which behavior ought to fall naturally has an important effect on the kind of examination we make of behavior patterns and the kinds of distinctions we find ourselves able to make among them.

In the quotation above we have translated as "smooth" (progression) Lorenz's word "stufenlose," which might be more literally translated "without steps" or "without levels." This is a gratuitous and very misleading oversimplification on Lorenz's part. The transition from protozoa to man is *not* "step-less." There are *characteristic* structural differences between phyletic levels, and these differences are responsible for *characteristic* differences in the organization of behavior. A protozoan is not like a simpler man. It is a different kind of organism, with behavior which depends in different *ways* on its structure. The analysis of behavior mechanisms at different levels (Schneirla, 1946) shows that it is frequently misleading to speak of *behavior* patterns or elements as homologous when they seem to serve similar (or the "same") functions and have superficially similar characteristics. Analysis of structural organizations out of which the specific behavior patterns emerge shows that similar behaviors at different phyletic levels often are end-products of evolutionary selection leading to the similar behavior, but deriving from different structures so that the underlying processes and mechanisms are not the same.

Lorenz's application of the concept of evolutionary change does not consist of analyzing the different ways in which behavior patterns at different evolutionary levels depend on the structure and life of the organism. It consists rather of abstracting aspects of behavior, reifying them as specific autonomous mechanisms, and then citing them as demonstrations of "evolution" in a purely descriptive taxonomic sense. Taxonomically, this procedure is often extremely valuable, but by its implicit assumption that "elements" of behavior maintain their nature regardless of change in the organization in which they are embedded (more properly, we should say from which they emerge), it hinders rather than helps analysis of the behavior patterns themselves.

Levels of Neural Organization

Lorenz characterizes each instinctive act as depending on a specific center in the central nervous system which continuously produces a type of excitation specific to the act, and which is partly "used up" when the act is performed. He uses the concept "used up" quite literally, even suggesting the existence of act-specific *substances* (Lorenz and Tinbergen, 1938). One of the principal types of evidence used by Lorenz to support this conception is the lowering of the threshold for release of the act as a function of lapse of time since performance of the act. That is, the longer the animal has gone without performing the act, the easier it is to elicit. This is taken by Lorenz as evidence of accumulation of the reaction-specific energy in the central nervous system. Lowering of the intensity of performance upon repeated elicitation is taken as further proof, since it may indicate the using up of the excitation faster than it can be produced.

Lorenz and Tinbergen offer observations along these lines on mammals, birds, fish, and insects. The hunting behavior of the dog (Tinbergen, 1942), food-begging of a young bird (Tinbergen and Kuenen, 1939), fighting in a fish (Tinbergen, 1942), courtship flights of a butterfly (Tinbergen, Meeuse, Boerema, and Varossieau, 1942) are all offered as examples of instinctive acts having this kind of physiological basis.

Lorenz and Tinbergen adduce as physiological evidence for this interpretation a series of studies by von Holst (1935–1937), on the mechanisms of locomotion in fishes. Von Holst observed that

almost completely deafferented fishes show some of the coordinations of locomotion. He concluded that the basic movement patterns of locomotion are the result of the accumulation of locomotion-specific energy in the central nervous system independent of peripheral activity, and are the result of a central (non-reflex) coordination.

In his original consideration of von Holst's work, Lorenz (1937b) stated that it would be premature to make positive assertions about the direct relevance of that work to his instinct theory. Lorenz and Tinbergen (1938), at about the same time, stated that the conception of locomotion as an example of instinctive coordination in Lorenz's sense might be a very rough simplification of the facts.

However, over the years since then, the relevance of this kind of evidence in their writings seems to have increased, although some doubt has been thrown on the validity of von Holst's conclusions. One might question the direct relevance of the neural mechanisms of locomotion in fish and amphibians to the explanation of the origins of complex "instinctive" behavior in birds and mammals. Tinbergen is aware of the dangers inherent in the procedure of using physiological evidence from lower evolutionary levels, lower levels of neural organizations, and simpler forms of behavior as analogies for the support of physiological theories of behavior mechanisms at higher and more complex levels. For example, after a description of this aspect of Lorenz's theory, Tinbergen (1948a) says: "These formulations are supported by the entirely independent investigations which have been conducted during the last ten years on the central nervous mechanisms of locomotion. Here, *to be sure on a lower level of integration* [my emphasis—D. S. L.], we are brought to a fundamentally similar position by the researches of von Holst, Weiss, Gray, Lissmann, and others."

In this case, Tinbergen's mention of the fact that the physiological evidence comes from a lower level of integration is actually embedded in an *expanded* use of these data to support theories based on observations at higher levels. This is merely a formal bow to the concept of levels, which appears to strengthen the form of the argument while actually weakening its content.

In point of fact, it is now doubtful whether even so simple a behavior pattern as locomotion, in so simple a vertebrate as a fish, is really organized in the way that Lorenz's instinct theory demands. Gray and Lissman (1940, 1946a, 1946b; Gray, 1939, 1950; Lissmann, 1946a, 1946b) have studied the effect of deafferentation on locomotion in fish and amphibians. Both regard their evidence as being against the probability of automatic-rhythmic production of coordinations in the central nervous system, even at the fish level, and even for locomotion. Lissmann, in fact, designed his experiments specifically in view of von Holst's observations, and explicitly in view of the use made of the latter by Lorenz. He concluded, on the basis of a *complete* afferent isolation of the central nervous system, that there was no central automatic production of excitation. It should be noted that the experiments of Weiss (1936, 1937a-d, 1941, 1950) support the conclusion that spinal centers in amphibians are so organized that the coordination of locomotor patterns is dependent upon characteristics of the centers. Gray and Lissmann's experiments, however, show that proprioception actually plays a major role in the normal ambulatory rhythms, even of these animals.

Tinbergen (1942) has expanded Lorenz's concept of neural organization to include higher levels of physiological and behavioral organization than the stereotyped "instinctive act" or consummatory act. Tinbergen conceives of instinctive behavior in general as being hierarchically organized in the individual. For example, in the reproductive behavior of the stickleback Tinbergen sees three main levels of organization, hierarchically arranged. The highest level represents the reproductive drive in general. This corresponds to a center at a high level in the nervous system which when activated (by external conditions, hormones, or autonomous cyclicity) sends impulses to a whole group of intermediate centers, making the latter capable of activity. Each of these intermediate centers corresponds to a behavior pattern involved in reproductive activities: fighting, nest-building, courting, parental behavior, etc. Each of these intermediate centers, in turn, activates (or contributes to the disinhibition of) a group of lower centers each of which coordinates a particular act which is released by an innate releasing pattern. For example, the fighting center, when activated by external stimulation (which can only occur when its threshold is lowered by activity in the superordinated center for the reproductive drive in general) puts the animal in "fighting mood" which makes possible the performance under proper stimulus-conditions of each of the acts

involved in fighting: biting, chasing, threatening, etc. The latter are the "consummatory acts" or "instinctive acts" of Lorenz. [N. B. The slight differences in terminology sometimes occurring between Tinbergen and Lorenz do not usually represent theoretical or conceptual disagreements.]

Tinbergen cites the work of Hess (1943, 1949) as demonstrating the reality of these autonomous centrally-coordinated centers of activity. By electrically stimulating various points in the hypothalamus, Hess was able to cause cats to perform sleeping, eating, and other behavior which was not related to specific external stimulation, and which ceased upon cessation of the stimulation. Tinbergen regards these observations, with those of von Holst, as demonstrating the reality of Lorenz's picture of centers of automatic-rhythmic production of action-specific excitation.

Hess found, however, that there was considerable variation in the responses to repeated stimulation of a specific spot in the hypothalamus. Stimulation of the same point might elicit quite different responses, depending upon the conditions of afferent inflow. This led Hess to conclude that there was not strict localization of function in the hypothalamus as (he assumed) there is in the cortex. [It might be pointed out that recent discussions of cortical function indicate considerable doubt about the reality of localized functions isomorphic with their behavioral expressions, even in the motor areas of the cortex (Lashley, 1923; Hines, 1947; Clark and Ward, 1948; Clark, 1948).]

Now, a strictly punctate localization of function is not necessary, either in cortex or in hypothalamus, in order that these organs be able to serve organizing and coordinating functions. In the light of Hess's work there is no doubt that the lower-level details and components of many behavior patterns are coordinated and integrated in the hypothalamus. But it is difficult to see how the shifting locus of this integration can be reconciled with the conception of a *center which produces an excitation* specific for the behavior patterns concerned. It is equally difficult to reconcile the fact that the function of a "center" depends partly on the type of afferent inflow present with the notion of the center as a place where excitation is produced for a particular kind of act.

Neither do the researches of Hess, nor those of Gray and Lissmann, support the idea that rhythmicity or cyclicity of behavior is a function of the periodic reaching of a threshold level of energy produced in such centers. As suggested by Gray and Lissmann, rhythmicity of behavior is much more parsimoniously explained in terms of periodic shifts in balance between central and peripheral processes or interaction between different central processes, than in terms of the production of periodic impulses by a single "center" which, in Lorenz's treatment, has the character of a "thing in itself."

Lorenz (1950) describes in some detail a hydraulic model, or analogy, of the instinct mechanism, including a reservoir of excitation and devices for keeping it dammed up (innate releasing mechanism) until appropriate keys unlock the sluices. Hydraulic analogies have reappeared so regularly in Lorenz's papers since 1937 as to justify the impression that they are not really analogies—they are actual representations of Lorenz's conception of the origin and channelling of "instinctive energy." [The basic assumptions—of a special center producing a reservoir of energy specific for each instinct, and of devices for distributing the energy—are very similar to those of MacDougall (1923, 1930).]

There is no neurophysiological evidence for such hydraulics in the brain. Aside from the controversial aspects of the idea of automatic-rhythmic production of excitation, such hydraulic conceptions simply do not conform with what we actually know about the complexities of brain function (cf. Fulton, 1949).

The actual physiological relationships underlying behavior patterns must be *analyzed* for the different behavior patterns concerned. The assumption which underlies Lorenz's approach to the neurophysiological basis of behavior is that the neural events underlying behavior patterns must somehow be isomorphic with the behavior itself. He is thereby led to assume that behavior patterns having similar functional characteristics must be caused by identical neural mechanisms. Lashley (1942) has pointed out the erroneous nature of such reasoning. It is by thus abstracting phenotypic resemblances in behavior at different levels, and by gratuitously transferring physiological explanations from one level to another that Lorenz creates the impression that "instinctive" acts are grounded in a common type of mechanism which is the same at different evolutionary levels.

Levels of Behavioral Function

As already pointed out, a serious question facing all investigators of animal behavior is the extent to

which different mechanisms may be assumed to be identical because of the apparent similarities in the behavior patterns they underlie. By this I do not mean to imply that the similarities may be unimportant, but only that functionally similar behavior patterns may be effectuated through very dissimilar causal mechanisms. And if the causal mechanisms hypothesized in the case of one of the behavior patterns are conceptually reified and applied to other patterns or other animals, because of the fact that the similar behavior patterns are subsumed under the same term or included in the same category or concept, the analysis of the mechanisms actually operating in the different cases is seriously hampered. Rather than making a developmental analysis of the processes concretely underlying each behavior pattern, the predominant tendency is to carry out brief studies on a variety of *selected* examples assumed to demonstrate the validity of the a priori "principle" or the reality of the hypothesized structure or "center."

This practice may produce very fallacious results. For example, both the amoeba and the neonate infant will move toward weak stimulation and away from strong stimulation (the amoeba as a whole, the child locally). In both animals, this serves the biological function of bringing the organism into contact with food (and for the child, protection), and away from contact with harmful stimuli. This similar biological utility is a sufficient basis of explanation for the evolutionary development of the similar modes of behavior in the two organisms.

But the *mechanisms* underlying the response in the two animals manifestly must be very different. In the amoeba, the differential response to weak and strong stimuli is caused by the differential effects of the weak and strong stimuli on the sol-gel relationship in the protoplasm of the single cell (Mast, 1926). In the neonate child, the basis is more obscure. Schneirla (1939) has suggested that initially it is the result of differences in arousal-threshold between flexor and extensor muscles of the limbs, so that they respond optimally to different impulse-frequencies in afferent volleys, corresponding to different intensities of stimulation.

These two behavior patterns may seem functionally quite analogous. Can we say that they are homologous? This would obviously be absurd. They represent two totally different kinds of adjustment, both selected (in the evolutionary sense) because they serve the same kind of function. Nor is there a "smooth progression" between the protozoan response and the human. At each level, the *mechanisms* underlying this characteristic and widely-distributed response (Maier and Schneirla, 1935) are derived from the specific structure of the organism in question. The behavior patterns are not homologous, although they *may* in some cases be based to different extents and in different ways on more or fewer homologous structures. The *analysis* of the behavior at each level must be in terms of its emergence from the structure of organisms at that level, as indicated in the examples of the amoeba and the neonate child, and *not* on superficial comparisons of the behavior with similar behavior patterns at other levels.

Lorenz's concept of "instinct" represents, I think, precisely this kind of undesirable reification of a hypothesized mechanism. Lorenz's use of the term "instinct" does not denote merely a group of behavior patterns characterized by certain common functional characteristics; it denotes a definite class of things—a specific group of homologous structures underlying acts *whose characteristics are isomorphic with those of the structures*. And the nature of the structures is inferred from the behavioral characteristics, supported by physiological evidence the inadequacy of which has already been pointed out.

This reification of the concept of "instinct" leads to a "comparative" psychology which consists of comparing levels in terms of *resemblances* between them, without that careful consideration of *differences* in organization which is essential to an understanding of evolutionary change, and of the historical emergence of new capacities. Thus the lowering of intensity of response as a consequence of repeated elicitation, in the case of certain sexual activities of a butterfly (Tinbergen, Meeuse, Boerema, and Varossieau, 1942) and of a fish (Tinbergen, 1942) is taken in both cases as verifying Lorenz's assumption of the nature of the organizing center for an instinctive act. The fact that some behavior patterns of a butterfly may exhibit functional similarities to some behavior patterns of a fish is interesting as an indication that similar response characteristics may be species-preserving in both cases. But it is not very judicious, and actually is rash, in view of the very different types of organization involved in the structure and the behavior of the two animals concerned, to assume that the mechanisms underlying the two similar response characteristics are in any way identical, homologous, or even similar, or that there is any historical (evolutionary) con-

tinuity between them *as such*. Yet this is precisely the basis of Lorenz's whole treatment of "instinct" and evolution.

In addition to distorting comparative study and the study of evolutionary change, this reification of "instinct" has unfortunate effects on the study of ontogenetic development. The development of an "instinctive" act inevitably appears to Lorenz to be the self-differentiation of a preformed, autonomous thing. Thus Lorenz sees the developing behavior of the animal as progressing *toward* the full-blown "instinct" rather than as developing *out of* interactions among processes present at that stage. This is a teleology which is inherent in Lorenz's approach, and which cannot be eliminated by his formal attempt to deny teleological and purposive procedures and to exclude the terminology.

For example, Lorenz mentions the development of fighting behavior in ducks. When fighting with another drake, an adult drake will grasp its opponent's neck in its bill and strike at him with a wing. Lorenz noted that ducklings whose wings had not yet feathered would perform the same movements even though the stubby, unfledged wing was not yet long enough to strike the opponent. Lorenz's interpretation (1937a) is that the instinctive act had matured before the full maturation of the structure which was used by it. This interpretation does not explain what the *duckling* is doing; rather, it prevents the investigator from seeing the problem of what it is about the duckling and its situation (and its ontogenetic history) which gives rise to this kind of behavior. This type of theory apparently causes the investigator to look at the process of development in such a way that the problem of the *origin* of this behavior, and its cause and role *in the duckling* are not considered by him at all. In the light of our previous discussion, it would appear that these are the crucial problems, and that a theory which makes them appear as relatively irrelevant to the explanation of the development of fighting behavior must be seriously lacking.

This conceptual merging of very different levels on the basis of superficial similarities permeates the system. For example, the concept of "taxis" as a meaningful class of behavior elements seems to be based on such a procedure. Lorenz defines a taxis as a movement which is continuously oriented with respect to the stimulus (thus distinguishing it sharply from an instinctive act which, once started, is centrally coordinated, independent of the receptors).

Tinbergen (1942) further classifies taxes into several categories, based partly on Kühn's (1919) analysis: (1) tropotaxis, equivalent to Loeb's tropisms, in which the animal turns until the relevant stimulus is equally intense on both sides; (2) telotaxis, a visual orientation based on fixation movements so that either eye can serve as the sole receptor; and (3) menotaxis, like telotaxis except that the orientation, instead of being toward the stimulus, is at a constant angle from it. To these categories of Kühn, Tinbergen added a fourth: pharotaxis, in which the animal is oriented to a part of the visual field defined in terms of its relation to the rest of the field, irrespective of the animal's orientation to the field.

This classification of "taxes" solely in terms of a highly restricted definition of the receptor processes inevitably lumps together many very different processes. For example, our amoeba and newborn infant both show a "turning-to" reaction to mild stimulation What possible category, based on the characteristics of the turning, could properly include both of these movements as examples of one kind of process? To say that the movement of the child and of the amoeba are both a taxis is to admit that the word "taxis" does not define a group of behavior patterns which have common mechanisms.

Tinbergen (1942) makes this explicit when he says: "... in the concept of pharotaxis the part played by mnemic processes is not taken as a criterion, because in tropo-, meno-, and telotaxis the criterion upon which the 'distinction' is based also leaves this topic out of consideration ... Menotaxis, for instance, can be innate or learned."

What then remains of Tinbergen's classification? Tinbergen himself is aware that the members of any of his taxis-categories probably differ widely in ontogenetic origin and central mechanism. How can the classification be justified? A preliminary classification has heuristic value only if the members of a given class are thought to be representative of similar dynamic processes which can be investigated. That, in fact, is the purpose which Tinbergen assumes for his classifications. But in the case of taxes, the classifications are known to contain different levels of organization and different processes. In this case the classification is based on the analogizing which appears to be basic to the Lorenz approach.

Lorenz (1939) and Tinbergen (1942) have both pointed out that, under the influence of natural selection, widely divergent species may develop

similar characteristics which should not be assumed to be homologous. Tinbergen (1948) gives an example of this "convergent evolution": "The most striking example of how far convergencies can go in these phenomena, is given by L. Tinbergen (1939) in his study of the mating behavior of the cuttlefish *Sepia officinalis*. Parallel with the development of eyes in cephalopods (convergent to those of fish) the courtship of the cuttlefish has evolved into a typically visual one closely resembling the courtship of certain sexually dimorphic fish, lizards, and birds. . . . This state of affairs closely resembles that found by Noble and Bradley (1933) in [the lizard] *Sceloporus*. In both species the male's display is primarily a means of threatening other males. . . ."

It will be noted that Tinbergen specifically notes that the resemblance is caused by convergence, rather than homology. However, his treatment of the behavior patterns involves the implicit assumption that the convergence is one of *mechanisms*. Actually, as far as we know, the convergence is only of *outcomes*. The assumption that the mechanisms underlying these similar outcomes are equally similar is both characteristic and gratuitous.

The Human Level

This analogizing and confusion of levels becomes patently shallow when either Lorenz or Tinbergen discusses human behavior.

For example, Tinbergen (1942) says, "The activation of other drives, too, leads to searching behavior. Classical examples are the searching for a nesting site in birds, for a house in man, etc." It is difficult to see what valid explanatory purpose can be served by such an inappropriate juxtaposition, based on the mere fact that the *outcomes* are similar *from the human point of view*.

Tinbergen (1942), speaking of "instinctive"acts which appear without external stimulation, as the result of extreme lowering of the threshold because of long non-elicitation, says, "Lorenz . . . discovered that various activities may occur in cases, where neither proprioceptive stimuli nor hormones could possibly be the driving causes. The simplest instance of this kind of vacuum activity is the hunting behavior of the well-fed dog. As every dog-owner knows, a dog can by no means be prevented from making hunting excursions by supplying it with ample food. Other instances of a similar kind are familiar to us by introspection. Sports, science and so many other activities certainly have connections with internal factors of this kind."

Here the implication seems to be that, because both are "spontaneous" and neither is mainly caused by proprioceptive stimuli or hormones (itself a gratuitous assumption), therefore the causes of hunting activity in the dog are the same as (or belong to the same class as) those of scientific activity in human beings! It is obvious that this argument is based on the most casual and unanalytical kind of comparison, and a lack of concern with the specific origins of the behavior patterns at issue.

Lorenz (1937b), speaking of the evolutionary relation between instinctive and learned acts, says:

> "The presence of an instinctive act also seems to be detrimental to the development of an intelligent process having the same function. At least, it is true of humans. To be convinced of the correctness of this statement, one has only to consider the behavior of highly intelligent men who have otherwise good critical faculties, when they 'fall in love' to carry out the undoubtedly instinctive reaction of mate-selection. The already-mentioned example of the ravens and jackdaws shows that higher psychological development may occur without any reduction of the instinctive, innate members of a behavior chain. . . ."

I include the last sentence to show how very easily Lorenz switches from man to bird without any apparent awareness that he is discussing phenomena which may be very different. The point of Lorenz's statement seems to be that men fall in love irrationally because "falling in love" is an instinctive reaction released by an innately-determined situation. In this case the unreality of the concepts used is apparent to any student of *human* behavior, although it may not be so to one of bird behavior—a fact which itself indicates that the source of the unreality lies partly in Lorenz's merging of different levels on the basis of superficial similarities.

Many other examples of Lorenz's interpretation of human behavior could be cited. For example (Lorenz, 1940), he interprets the relative attractiveness to women of several breeds of dog in terms of the degree to which they fit the innate perceptual pattern releasing instinctive maternal behavior in the human individual! This, again, is entirely derived from a too facile analogy with less complex kinds of animals. Recent work with chimpanzees reared in darkness (Riesen, 1947) and with congenitally blind human beings whose sight had just been restored by surgery (Senden, 1932) indicates

that, at least at these phyletic levels, any response to or perception of visual shapes, proportions, sizes, and relationships can only occur as the result of a long and complex learning process. Under these circumstances it is most difficult to assign any meaning whatever to Lorenz's assertion that these responses are based innately on perceptual characteristics of shape and proportion (Hebb, 1949). [Lower mammals apparently require less learning for the establishment of some of their characteristic modes of response to the visual field (Hebb, 1937a, 1937b; Lashley and Russell, 1934).]

The interpretation of human behavior in terms of physiological theory based on lower levels is carried one step further when Lorenz (1940) equates the effects of civilization in human beings with the effects of domestication in animals. He states that a major effect is the involution or degeneration of species-specific behavior patterns and releaser mechanisms because of degenerative mutations, which under conditions of domestication or civilization are not eliminated by natural selection. He presents this as a scientific reason for societies to erect social prohibitions to take the place of the degenerated releaser mechanisms which originally kept races from interbreeding. This is presented by Lorenz in the context of a discussion of the scientific justification for the then existing (1940) German legal restrictions against marriage between Germans and non-Germans.

The directness of Lorenz's application of the concept of innate releasers to human social relations may be gaged by the following quotation (1940): "The face of an Asiatic is enigmatic to us because the physiognomic characteristics to which our innate perceptual patterns respond are not connected with the same behavioral characteristics as in our race. . . . In all likelihood, this function (of recognizing facial characteristics) cannot be substituted for by experience, as has been determined by many people who are acquainted with foreign races."

Social psychologists will all agree that the various degrees of difficulty which different people have in learning to recognize and respond to facial expressions in a culture different from their own is at least partly dependent upon the attitude with which they approach the strange culture to begin with.

The Sources of Motivation

Lorenz states that as the level of action-specific energy in the central nervous system rises the animal is set into activity. He says (1937b), "It is one of the most important and most remarkable features of the instinctive act, that the organism does not wait passively for its release, but *actively seeks these stimuli*." This active seeking is called "appetitive behavior" (Craig, 1918). It may range from simple turning movements ("taxes") to the most complicated kinds of intelligent behavior. As has already been pointed out, Lorenz regards these as being continuous with each other, both being (at different stages of evolutionary development) means of bringing the animal into a situation containing the stimuli which will release an instinctive act (viz., eating, copulation, etc.).

Lorenz recognizes a few instances of motivation the source of which is peripheral (viz., hunger, defecation, etc.). But he adopts the characteristic procedure of lumping together all "goal-directed" (i.e., adaptive) behavior which does not have an immediately obvious peripheral motivation under the rubric of "appetitive behavior." His conception of "peripheral sources of motivation" is practically limited to the examples just given. I do not recall any reference in any of the writings of either Lorenz or Tinbergen to the autonomic nervous system, or to the possibility of qualitatively different roles of the autonomic nervous system at different phyletic levels, or to the possibility of complex peripheral changes caused by hormones, as sources of motivation (cf. Beach, 1948). One result is that the referring of motivation to the action-specific "centers" in the central nervous system is often like the concept of "innate behavior" itself, simply a substitute for actual analysis of the biology of the specific case. For example, Tinbergen (1951) says that injection of prolactin into a dove has two effects: (1) it causes development of the crop gland, and (2) it causes brooding behavior. It is thus more or less taken for granted that the behavioral effect of the hormone is somehow a specific one; developmental analysis of relationships between broodiness and crop-gland or brood-patch stimulation is excluded by the nature of the instinct theory, and of the consequent theory of motivation. In the case of "dominance" behavior in the chimpanzee Birch and Clark (1950) have shown that behavioral effects of hormones may actually be mediated by peripheral structures in situations where it is not at all apparent a priori that "proprioceptive stimuli" can play a role.

Lorenz regards all purposive (adaptive) behavior as being directed toward the performance of the instinctive acts. For Lorenz, it is the *performance of*

the instinctive act itself which serves as the animal's goal. Thus he says (1937a):

> "... in a man working with the motive of getting food, the behavior directed toward this goal includes many of the higher psychic performances of which he is capable; the 'motive' (goal)—the instinctive act of 'biting and chewing'—has become drawn back to the end of a long series of acts, without, however, thereby in any way denying its fundamentally instinctive nature."

Thus to Lorenz, the statement "man works in order to be able to have released [by food] the instinctive act of biting and chewing" is the *same* kind of statement as "the frog turns to the right in order to be able to have released [by the sight of a fly in front of him] the instinctive act of flipping out his tongue." He regards these two goal-directed behavior patterns as being (in the evolutionary sense) continuous with each other, and both as having the same kind of relationship to the instinctive act which is the end-member of the behavior chain. However, such a formulation is misleading and of little heuristic value. The actual complexity and variety, and situational relevance, of the sources of human motivation make such statements meaningless, not merely because human motivation is more complicated than that of the frog, but because it is qualitatively different in organization and development.

Tinbergen's equation of the causes of sports and scientific activity with those of hunting in the dog, because both appear to be internal and "self-exciting," is perhaps an extreme example of the result of analogical methods of approach, and of the belief that every behavior must have some center isomorphically corresponding to it in the nervous system.

HYPOTHESIS AND OBSERVATION

The "Innate Releasing Mechanism"

It may be instructive to examine some ways in which Lorenz's theoretical approach is expressed in an investigation of behavior.

Tinbergen and Kuenen (1939) studied the stimulus situations eliciting and directing the gaping (food-begging) movements of young thrushes. The gaping movement consists at first of vertically directed stretching of the neck, and opening of the mouth. The birds are blind at hatching; their eyes do not open until about 9–10 days of age. During this first blind phase gaping can be most easily elicited by tapping or jarring the substrate. When the eyes first open the bird normally lies with its eyes closed, and opens them only when it is gaping. Tinbergen and Kuenen state that the bird will gape in response to a moving visual stimulus as soon as the eyes open, and that the innate releasing pattern for gaping therefore includes visual stimulation. For the first day or so after the eyes open gaping is not *directed* toward a visual stimulus; even though the stimulus will elicit gaping, the gaping is still directed vertically upward. However, after about one day the gaping begins to be directed toward certain defined parts of the visual stimulus (highest, nearest, break in outline, etc.).

Tinbergen and Kuenen's conclusions are that the "centrally-coordinated" instinctive act and the (continuously-directed) taxis mature at different rates, the taxis not maturing until 10 days or so of age while the instinct is fully mature at hatching. In addition, they conclude that the adequate stimulus-situations for releasing and for direction of the act are different, and are both innate.

First, a word about the "maturation of the taxis." It is not clear why the animal's experience during the first day after its eyes open is not an adequate reason for its development of orientation toward the visual stimulus. Tinbergen and Kuenen maintain in their discussion that some of the specific features of the stimulus toward which orientation occurs are not learned by direct experience. However, it is not clear that the *orientation* toward the visual stimulus is not a result of experience. Even their limited discussion of possible learning is based on inferences from incidental observations, indicating that Tinbergen and Kuenen's orientation toward Lorenz's theory led them to discount the serious possibility of learning being involved.

The "innateness" of response to moving visual stimuli is quite ambiguous. It will be recalled that the birds lie with their eyes closed for much of the time just after their eyes have first opened. I quote from Tinbergen and Kuenen's protocols:

> "5/26/36. Black Thrush, 9–10 days. Lifting and moving back and forth of the wooden covers evokes no reaction. They gape immediately to a tap on the nest. When the gaping subsides, we move our hand back and forth over the nest, and the birds instantly beg strongly.
>
> "Later on the same day: Tap on the closed box releasing gaping. Subsequent lifting of the cover does not; the eyes are closed. Tap causes gaping. After cessation of the reaction, the animals remain lying with open eyes. We hold over the nest, one after the other: a black disc, a white wooden rod ... and a black wand.... All the objects are reacted to by violent gaping.
>
> "5/10/36. Song Thrush, 10 days. Preliminary lifting

of the cover causes no reaction; light tap does. After the birds begin to calm down, a finger shown over the nest immediately releases gaping."

It is apparent that normally the *first times that young thrushes see visual stimuli they are already in a state of gaping excitement*, since at first their eyes are open only when they gape.

I have verified these findings on young red-winged blackbirds (*Agelaius phoeniceus*), on which I could repeat all of Tinbergen and Kuenen's observations. However, I was able by watching the birds for several consecutive hours to note several occasions on which one or another of the birds was lying quietly with its eyes *open*, when it had not recently gaped. Such birds would *not* gape in response to a moving finger above the head, although they might move their heads to fixate the finger. If I tapped the nest, thus causing gaping, and then moved my finger over the birds when gaping was subsiding, or shortly thereafter, the bird would gape instantly and vigorously. What is meant then by the statement that the birds gape "innately" to visual stimulation? It would be easy to produce ad hoc assumptions about temporary changes in threshold of the innate releasing mechanism as a result of tactual stimulation. But these must be recognized as ad hoc. The possibility should be recognized that any stimulation to which the bird is sensitive will increase the activity of the bird when it is already gaping, and may become associated with gaping, so that the later-apparent specificity of response to visual stimuli may be a consequence, not of innate connections, but of the conditions under which visual sensitivity normally first becomes possible. In addition, these birds must be fed almost every hour, and the possible relevance of association of visual stimulation with food reinforcement should not be overlooked. In this connection we may note the experiments of Padilla (1930), who found that chicks that were kept in the dark and force-fed for the first twelve days of life, so that they had no opportunity to associate pecking behavior with visual stimuli or with food, would when placed in a normal feeding situation starve to death without ever giving any sign of the allegedly "innate" pecking behavior.

It should be noted that the conditional nature of the effectiveness of visual stimuli is indicated by Tinbergen and Kuenen's own protocols, but that evidently these authors have not really considered these facts. This, I think, is because they are a priori convinced that the developmental process is a maturational one, and that they therefore do not have to analyze its conditions. The Lorenz theoretical approach tends to restrict the recognition of significant details and to obscure possibly relevant features of developmental processes.

Many cases of "innate releasing mechanisms" seem to suffer from a similar approach. It will be recalled that the innate releasing mechanism is regarded as a "preformed neural mechanism" (Lorenz and Tinbergen, 1938) for the release of the instinctive act. Tinbergen refers to the releasing stimuli as "sign stimuli" because they "represent" the biologically appropriate object of the instinctive act. One might ask "Sign of what? Sign to whom?" There is a subtle anthropomorphism about the concept of innate releasing mechanisms which is not at first apparent. For example, Lorenz and Tinbergen (1938), in discussing the egg-rolling of the gray goose, speak of an innate releasing pattern corresponding to the situation "egg outside the nest." Now, "egg outside the nest" is *not* the perceptual situation to the bird—it is the perceptual situation to the human observer. When Lorenz and Tinbergen investigate the effective features of the situation, they are looking for a pattern of stimuli corresponding to a "pattern" which they presume to exist in the central nervous system. Consequently, there is never any analysis of any possible *specific* relationships between effective stimuli and the structure or physiology of the organism concerned. Thus the described stimulus-situations become structured in human terms (bird of prey, vegetation, the parent's head, etc.) instead of in terms indicative of the problems of specific relationships between the structure and function of the animal being investigated. This approach, again, derives from Lorenz's identification of every behavior pattern with a specific hypothetical "center," rather than with the coming into play of specific structural-functional relationships, which may be very different in different kinds of organisms and for different behavior patterns.

For example, Tinbergen (1948b) says: "The escape reactions of many birds from passing birds of prey are a response to a type of movement and to a special characteristic of shape, namely, 'short neck.' " Now, it is certainly true that many birds perform "escape" movements at the sight of a "short-necked" bird flying overhead (Krätzig, 1940). But Tinbergen says "short-necked" rather

than, for example, "having a short and long projection at opposite ends, and moving so that the short projection is anterior." His usage is, of course, more convenient, as he makes clear. But in addition it derives from, and in turn reinforces, the Lorenzian notion that the "short-neckedness" is a perceptual "sign" or "sign stimulus" (Tinbergen, 1939) which corresponds innately to a preformed neural "releasing" mechanism. Instead of leading to an analysis of the specific patterns of excitation of sensory elements in the bird's eye which are required for the elicitation of the response, and a further consideration of the effect of such patterning on central nervous activity in the nervous systems of these birds, Tinbergen's terminology requires the identification of the bird's readiness to perform "escape movements" with a preformed "conception" of the short-necked character of hawks. Thus, "the partridge runs for cover from an overhead object with a short neck," and "the goose rolls back to the nest an object lying near the nest which is smooth-contoured and hard-surfaced," become not *definitions* of the problem of how the structure of the various birds makes it possible for them to react to their environment, but rather *solutions* to the question: "What are the characteristics of these two members of the class of innate releasing mechanisms?" The essential assumption of Lorenz's approach is that these two types of behavior are related to environmental stimuli by means of mechanisms that are basically identical except for the perceptual details themselves. When extended (as it is) to the whole animal kingdom, this approach becomes profoundly anti-evolutionary, in spite of Lorenz's concern with "comparative" studies.

Lashley (1949) has noted with some approval Lorenz's studies of releaser patterns. For example he has said:

> "A study of complex instincts requires a detailed analysis of the exact stimulus or combination of stimuli which call forth the behavior, combined with descriptions of the behavior elicited. This has been attempted under controlled conditions only for some instinctive behavior of birds (Lorenz, 1935)."

However, a closer examination of Lashley's concepts and those of Lorenz will show that the subsequent development of Lorenz's approach was not at all in the direction anticipated by Lashley. Lashley (1949) says:

> "The nesting tern seems to notice no difference when her eggs are dyed . . . but is . . . disturbed if their . . . contour is altered by sticking on a bit of clay or putty . . . smoothness of outline is the essential character of the egg. This is the sort of property that can be most easily interpreted in terms of the inherent tendencies to functional organization in the nervous network.
>
> "I do not mean to imply by this that the geometry of the web of the spider is exactly represented in the spider's brain. . . . The angle of radii may be determined by the angle at which the legs are held (Peters, 1937); the completeness or incompleteness of the orb may depend upon the readiness with which certain postures are assumed in relation to gravity. . . . The simple nest of the rat is piled and pushed about until it satisfies certain sensory requirements of reduced heat loss. The orb of the spider is perhaps a composite of such sensory requirements combined with some specialized geometrical perceptions such as are illustrated by the rat's more ready recognition of a . . . circle than of irregular ink blots."

In contrast to this approach, Lorenz (1935) has used the analogy of a key unlocking a lock, to describe the function of the releasing pattern in releasing an instinctive act. To pursue this analogy, Lashley would regard it as the task of the locksmith-investigator to investigate all the characteristics of lockopening devices, including keys, picklocks, and any other means of opening the locks; and to consider these characteristics together with what he knows of the structure of locks, the conditions of their use, their history, etc., in order to gain an understanding of how the functions of the various kinds of locks are related to their structure. To Lorenz on the other hand, all the locks are basically alike, so that investigations of the characteristics of the keys required to open them reveals nothing about internal differences among lock mechanisms, but only about the specific arrangement of tumblers in each lock.

All of this should not be taken to mean that we do not recognize that relatively simple stimuli may sometimes lead to the appearance of quite complex behavior. As a matter of fact, some of the best studies of stimulus-conditions eliciting various types of animal behavior have been carried out by Lorenz and Tinbergen and their associates (e.g., Tinbergen and Perdick, 1950). The point is not to deny the existence of simple stimuli which under some conditions lead to complex behavior. Rather, it is that the assigning of the locus of activity to a hypothetical center in the brain, with characteristics predeterminedly and isomorphically corresponding to those of the stimulus situation, represents an unphysiological way of thinking disguised in physiological terms.

"Vacuum Activities"

The so-called "vacuum activities" or Leerlaufreaktionen are regarded by Lorenz and Tinbergen as evidence of the accumulation of reaction-specific energy in the instinctive center until it "forces" its way through the inhibiting innate releasing mechanism and "goes off" without any detectable external stimulus.

Lees (1949) has cited the example of the cyclical colony activities of the ant *Eciton hamatum* (Schneirla, 1938) as an example of "something akin to 'vacuum activity.'" Colonies of this army ant pass regularly through *statary* and *nomadic* phases, each lasting about 20 days. As Lees points out [based on Schneirla's (1944) description]:

> "During the statary phase the bivouac, to which the single queen is confined, remains *in situ* and raiding activities are minimal. During the nomadic phase the position of the bivouac is changed each nightfall and strong raiding parties emerge from the colony. This activity is in no way related to the abundance or scarcity of food in the neighborhood. . . ."

This cyclic behavior thus appears to Lees to have the character of a "vacuum activity," in that it occurs periodically without any noticeable change in the external stimulus-conditions. This is very misleading, for Schneirla's (1938, 1944) analysis of this behavior has shown that the change from statary to nomadic behavior is a consequence of the growth of a great new brood of ants. When the callow workers emerge from their cocoons, their movements stimulate the adult workers to great activity. As the callows mature and cease to be dependent on the adults, their energizing effect is lessened. At this point, the emergence of wriggling larvae from the eggs supplements the diminishing activating effect of the callows on the adults. When the larvae pupate, and become inactive, the adults are no longer subject to trophallactic (Wheeler, 1928) stimulation, and the colony changes to its statary period.

The point that is relevant to our discussion is that Schneirla's analysis leads to a conception that is the *opposite* of that implied by the notion of "vacuum activity." The periodic recurrences are *not* the result of the building up of energy in any animal's nervous system. They are the result of the periodic recurrences of inter-individual stimulating effects. The behavior is not represented "in advance" in *any* of the animals in the colony; it emerges in the course of the ants' relationships with one another and with the environment. There is no "reaction-specific energy" being built up. The periodicity is a result of the periodicity of the queen's egg-laying, which is *not* a "center" having *any* characteristics corresponding to the behavior. And even this is not a *direct* relationship. If the number of larvae in a colony is experimentally reduced by 50 per cent, thus reducing their total stimulating effect, a normal nomadic phase cannot occur. Recent findings (Schneirla and Brown, 1950) have in fact confirmed the hypothesis that each of the regular large-scale egg-delivering episodes in the queen's function basic to the cycle is a specific outcome of her over-feeding, due to a maximal stimulation of the colony by the brood. This event, occurring inevitably at the end of each nomadic phase, is a "feed-back" type of function, not at all related to the implications of "vacuum activity."

The restrictive nature of such categorical theories as that of Lorenz is very well illustrated by Lees' remarks on *Eciton*. The actual development process leading to the periodic performances of this ant are well understood, and are *known* to have no essential relationship to any "reaction-specific energy" in any nervous system; further they are *known* not to be "innate" as such (Schneirla, 1938). The processes leading to this behavior surely have nothing to do with the processes leading to "vacuum activities" in a fish. Yet the superficial similarity is sufficient to cause Lees to cite the ant's behavior as an example of a type of behavior described for vertebrates. This is a good example of the tendency encouraged by such theories to look for cases fitting the theoretical categories in many types of behavior, rather than analysis of the processes involved in the development of any one behavior pattern.

CONCLUSION

We have summarized the main points of Lorenz's instinct theory, and have subjected it to a critical examination. We find the following serious flaws:

1. It is rigidly canalized by the merging of widely different kinds of organization under inappropriate and gratuitous categories.
2. It involves preconceived and rigid ideas of innateness and the nature of maturation.
3. It habitually depends on the transference of concepts from one level to another, solely on the basis of analogical reasoning.
4. It is limited by preconceptions of isomorphic

resemblances between neural and behavioral phenomena.

5. It depends on finalistic, preformationist conceptions of the development of behavior itself.

6. As indicated by its applications to human psychology and sociology, it leads to, or depends on, (or both), a rigid, preformationist, categorical conception of development and organization.

Any instinct theory which regards "instinct" as immanent, preformed, inherited, or based on specific neural structures is bound to divert the investigation of behavior development from fundamental analysis and the study of developmental problems. Any such theory of "instinct" inevitably tends to short-circuit the scientist's investigation of intraorganic and organism-environment developmental relationships which underlie the development of "instinctive" behavior.

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Present address: Rutgers University, Newark 2, N. J.

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PROBLEMS OF ORIENTED GROWTH AND STRUCTURE IN PHYCOMYCES

By EDWARD S. CASTLE

Biological Laboratories, Harvard University

INTRODUCTION

SINCE the classic studies on the cultivation and growth of *Phycomyces* by Carnoy (1870), interest in the behavior of this remarkable fungus, though always centered in Belgium and the Netherlands, has spread more widely. It is true that, contrary to the expectation of one of its early partisans, *Phycomyces* has not taken its place beside the frog as one of the commonest laboratory objects. Nevertheless, in the succeeding years this fungus has served in a number of surprisingly different and important investigations. Its large, spore-bearing cells have supported many investigations of plant tropisms, especially phototropism; it was the vehicle for Blakeslee's pioneer work on heterothallism in the moulds; and, more recently, *Phycomyces* was prominent in the discovery of vitamin dependency in the nutrition of fungi.

Still another aspect of the life of this organism, and the one to be brought under consideration in this review, is its habit of so-called spiral growth, a subject of investigation for a little over twenty years. At first sight a mere botanical oddity, this phenomenon has attracted the attention of a number of students of growth and of wall structure. In spiral growth the tubular plant cell both extends and twists itself, by active growth in area of the cell wall, along an axis which winds helically through the localized growing zone, much like the spiral wrappings of a cardboard mailing-tube. Because of the free, unencumbered aerial growth of the sporangiophore of *Phycomyces* with the resulting possibilities of measurement and manipulation, and because of the central position held by the problem of directionally oriented growth for theories of cell-wall structure and of wall growth, a brisk tempo of investigation, speculation, and even of controversy has lately resulted. The present review will center about work done with *Phycomyces* itself, chiefly because the directional aspects of growth in single cell membranes have elsewhere hardly been directly studied at all. A more inclusive survey of the field has recently been given by Preston (1952). Definite answers to some of the most fundamental questions are still lacking; the reviewer will not attempt forcibly to fashion these answers, but rather to grope, on the evidence available, in the general direction of understanding.

PHASES OF GROWTH

The asexual developmental history of *Phycomyces* is well known (Errera, 1884) and may be briefly summarized as follows: Following germination of a spore on a suitable medium, preferably solid, a luxurious mycelium develops within a few days, and subsequently gives rise to numerous aerial sporangiophores. These are unbranched, tubular cells without cross-walls which grow up from primordia formed by the mycelium close below the surface of the substrate. For a day or two each sporangiophore grows at its tip, sensitive to gravity, to light, and to other environmental agencies or gradients; the tubular cell may easily have a diameter of 100 μ, and may in this phase grow to a length of several centimeters. Next, growth in length ceases, the apex of the tip balloons out into a not quite spherical swelling full of yellow pigment and densely granular protoplasm: this is the forming spore mass, which the laying down of a cross-wall, the columella, cuts off ultimately from continuity with the fluid-filled cavity of the sporangiophore; the spore mass then cleaves into a large number of spores, and the mature sporangium, darkening to brown and to black, is henceforth borne as an isolated load at the top end of the sporangiophore. Now the sporangiophore again commences to elongate, by growth occurring exclusively in a zone 1 to 2 mm. below the sporangium, and at a more rapid rate than earlier;

this "grand period" of growth may proceed for hours and even for days thereafter, and is the phase of growth which has particularly been put to experimental use. The several stages of growth and morphogenesis are depicted in Fig. 1, based on the systematic observations of Errera (1884) and slightly modified by Castle (1942). The numbers there assigned to the various stages are generally accepted, and reference to them will be made throughout the present discussion.

SPIRAL GROWTH

The phenomenon of spiral growth of the sporangiophore appears to have been first noted by Burgeff (1915), and first closely studied by Oort (1931). The mature sporangiophore (stage 4b) elongates for a relatively long period of time, and at rates often as high as 3 mm. per hour at 25°C. As it elongates, the terminal spore mass, if suitably marked with glass fibers or attached particles, may be seen to rotate about an axis which is the long axis of the sporangiophore. In fact, the cell is not only elongating but also twisting its terminal end during growth, so that the orientation of growth in the enlarging cell membrane is along a steep helical axis inclined, in individual cells, from a few degrees to as much as 40° from the longitudinal axis of the sporangiophore (Oort, 1931; Castle, 1936a; Roelofsen, 1950a; Middlebrook and Preston, 1952b). This steeply spiral orientation of the axis of growth, originally calculated from simultaneous measurements of elongation of the sporangiophore and rotation of its tip, is visibly confirmed by patterns of helical striations in the mature wall (Castle, 1938a) and in the growing zone itself (Roelofsen, 1950b). All observers have agreed with Oort's original conclusion that the almost universally preferred direction of spiralling is "left-handed" (although he denoted it otherwise) meaning that the sporangium viewed from above rotates clockwise; only rare individual cells in stage 4b exhibit counter-clockwise rotation (Oort, 1931; Castle, 1936b; Preston and Middlebrook, 1949).

It is the causal mechanics of this spiral mode of growth that has attracted attention, and there is some evidence that the phenomenon, though conspicuous in *Phycomyces*, is of more general occurrence (Astbury and Preston, 1940; Castle, 1942). The relation between orientation of structure in the growing, primary wall and orientation of the growth process has been of particular interest, enhanced by recent studies of the wall structure of *Phycomyces* by electron microscopy (Frey-Wyssling and Mühlethaler, 1950; Roelofsen, 1951a; Middlebrook and Preston, 1952a). It must be borne in mind that growth of the primary wall—growth in surface area, cell extension—is most likely a radically different process from thickening and spiral layering in secondary walls, so well known in a wide variety of plant cells (e.g., Bailey, 1940). The formation of spiral structure in secondary walls, therefore, may have little or no relationship to the processes here under consideration.

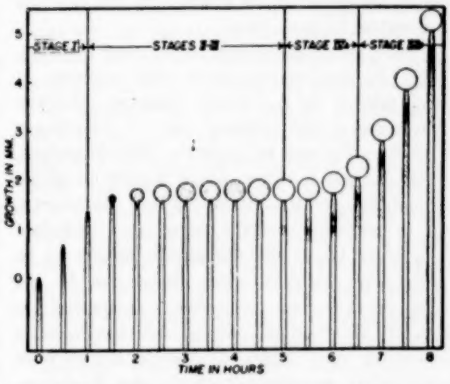


FIG. 1. DEVELOPMENTAL STAGES OF THE SPORANGIOPHORE OF PHYCOMYCES

Areas stippled where growth is occurring. The rotational component of spiral growth is not shown: in stage 4a it results in temporary *counterclockwise* rotation of the sporangium seen from above, in stage 4b in *clockwise* rotation. Growth in this last, principal stage is rapid and may last for days; only the first hour-and-a-half can be shown in the diagram.

THEORIES OF SPIRAL GROWTH

Theories of the mechanism of spiral growth in *Phycomyces* may be placed in two broad categories: (1) those that attribute the origin primarily to protoplasmic activity of some sort, not always well defined; and (2) those that look to existing oriented wall structure, in whole or in part, for its immediate source. Such a classification is somewhat arbitrary, since few today would deny that the primary, growing wall of the plant cell is a structured but heterogeneous system, drenched with protoplasm, in which microfibrils are being formed and interconnected by processes ultimately geared to cellular metabolism. In spite of the general acceptance of such a point of view, proponents of theories of spiral growth have shown a nostalgic

fondness for argument about whether the horse really comes before the cart.

"Protoplasmic" Theories

Since spirally streaming protoplasm is conspicuous in the older but not-growing, more basal regions of the sporangiophore, it was early wondered whether oriented streaming might not align fibrils or chain molecules being built into the primary wall (Oort and Roelofsen, 1932; Castle, 1936b; Pop, 1938). There are now sufficient reasons for believing that this cannot be the case, and the suggestion in its simple form has received no attention for some time.

A more recent interpretation by Frey-Wyssling (1952) invokes protoplasmic determination of spiral growth in a different manner. Electron microscopy of the primary wall of *Phycomyces* (Frey-Wyssling and Mühlethaler, 1950; Roelofsen, 1951a) reveals a rather dense texture of chitin microfibrils, perhaps lamellated and interwoven, with a generally isotropic outer layer underlain by a layer where the microfibrils appear to be statistically oriented nearly transverse to the cell's axis, or to cross each other at an angle of less than 90°. This finding confirms and extends, in an interesting way, earlier conclusions drawn from polarization microscopy (Oort and Roelofsen, 1932; Castle, 1938a). From the complexity of structure revealed in such electron micrographs of the primary wall, Frey-Wyssling (1952) now concludes that "there is no main direction which could be declared as the pitch of a spiral" in this primary wall. Since he also believes that enlargement of the wall in area and intussusception of new structural elements can only occur by loosening of the microfibrillar mesh at local spots, he is led to conclude further that "it must be the living protoplast which causes spiralling and not the texture of the cell wall which is rather the consequence than the origin of spiral growth." As to mechanism, he suggests that "the spot where the primary wall is loosened for the intussusception of new microfibrils must be rather small in area and move about. If this movement is a rotation the result must be spiral growth as elongation takes place at the same time."

Yet by attaching a single, small particle to the wall of the growing zone in *Phycomyces* and following its relative displacements longitudinally and rotationally during growth, it was shown (Castle, 1937a) that a precise axis exists throughout the length of the growing zone, and that this is a helix of constant pitch. This fact, structurally confirmed by striations in the wall left by the process of growth (Castle, 1938a; Roelofsen, 1950b), tells us that growth is oriented along and takes place parallel to such an axis throughout the whole growing zone of the cell—a length of usually about 2 mm. in the mature sporangiophore (stage 4b). The suggestion by Middlebrook and Preston (1952a), repeated by Preston (1952), that growth in these cells normally occurs only in a very small region immediately below the attachment of the sporangium is contrary to all the known facts. Moreover, these same studies (Castle, 1937a) reveal the distribution of the *intensity* of growth over the zone in which it takes place, showing that it rises to a maximum about 0.3 mm. below the attachment of the sporangium and then declines to zero as the lower end of the zone is reached. Such facts seem truly incompatible with Frey-Wyssling's view of spiral growth as determined by a wandering of the protoplasm, or with his opinion that cells generally show enlargement in surface area only in small localized regions. Inferences as to the possibilities of growth drawn from an examination of structure, rather than from the study of growth itself, can be seriously misleading. Frey-Wyssling's interpretation of the mechanism of spiral growth in *Phycomyces* has already been challenged by Roelofsen (1951b), and must be judged contrary to known facts.

"Structural" Theories

The second group of theories ascribes a major or exclusive role in the mechanism of spiral growth to existing wall structure, itself preferentially oriented as shown by optical and elastic anisotropy of the primary wall, and by the average course of chitin microfibrils in electron micrographs. There is, for example, overwhelming evidence, largely due to the earlier work of Frey-Wyssling (1935), that cellulose or chitin fibrils in the primary wall of growing cells of tubular shape have, statistically, a preferred orientation more nearly transverse to the axis of elongation than parallel to it. This is the fact responsible for the now well-known negative birefringence, in surface view, of the growing regions of tubular cells generally.

Of all the theories which look to the properties of the cell wall as the cause of spiral growth, that of Heyn (1936, 1939) is the most strictly deterministic. He suggested that structural peculiarities

of crystalline chitin in the wall might lead to enlargement along slip-planes in the crystal lattice of this substance, obliquely inclined relative to the cell's axis, resulting in spiral growth. Unfortunately, it is impossible to reconcile this idea with such facts as: (1) the known variation in angle of spiral growth from cell to cell; (2) the change of angle with change of temperature; and (3) the mesh of chitin microfibrils shown by electron microscopy to be present in the primary wall. Heyn's suggestion has received no recent consideration.

A very explicit hypothesis, based on the not unreasonable assumption that some important connection exists between growth and wall structure, has recently been developed by Preston (1948; Preston and Middlebrook, 1949; Middlebrook and Preston, 1952a, b). This theory is conveniently summarized in Preston's recent book (1952), and its chief features will be set forth here only qualitatively. The structural skeleton of the growing cell wall is considered to be formed of spirally-wound chitin fibrils obliquely oriented, on the average, at a small angle from the transverse axis of the sporangiophore. The elastic properties of this structural helix are compared to those of a coil spring fixed at one end and extended by a load hung on the free end. When so loaded, a coil spring extends elastically and at the same time the free end rotates so that the winding coils up on itself (see, however, Roelofsen, 1949, 1950b). Preston offers this model as an imitation of how spiral growth may occur in the sporangiophore, the spiral structure of the wall being under the stress of turgor pressure, and extension and growth occurring with a rotary component comparable to that shown by the coil spring. He has particularly sought support for this theory by measurement of the elastic properties of chitin fibrils, and by substitution of values for these in equations describing the behavior of coil springs under static load.

The reviewer is not sufficiently schooled in statics to judge the fundamental physical reasonableness of the analogies here proposed, and will confine himself to certain general observations regarding Preston's interpretation, in addition to offering some specific criticisms of it. In the first place, Preston's model is acknowledged to be static, like earlier mechanical models proposing to imitate the origin of spiral structure (Castle, 1937b; van Iterson, 1943). The actual, dynamic processes of growth—the building, application, or insertion of new elements of wall structure—must be accounted for by hypotheses subsidiary to the main idea of elastic deformation of spiral structure in the wall. It may also be noted that no explanation is offered as to how spiral structure came to exist in the wall initially with the preferred orientation which it displays.

Preston's theory is forthright in demanding the *net* orientation of structure in the growing wall to be along a flat, left-handed or "S" spiral, since in his model experiments only springs so wound showed, on extension, a rotation similar to that normally found in *Phycomyces*—namely, clockwise rotation of the sporangium seen from above. Roelofsen, to whom we owe the original studies of wall structure in *Phycomyces*, has reinvestigated this question by direct optical studies and by several other methods (Roelofsen, 1950a, b, 1951a). The point at issue, whether structure in the growth zone is oriented predominantly in a flat left-handed ("S") spiral or in a flat right-handed ("Z") spiral, is difficult, perhaps impossible, to settle by ordinary observational methods, as the writer knows from personal experience. He is impressed, therefore, by the varied evidence adduced by Roelofsen in favor of a "Z" spiral structure; studies of birefringence, themselves perhaps indecisive; studies of the twist of tubes with spiral structure subjected to internal pressure; studies of the direction of elastic twist in the sporangiophore itself with artificially raised internal pressure; and unequivocal demonstration, by microdissection, of the unwinding of flat "Z" spiral strips from the cell wall of the growth zone of the sporangiophore. Middlebrook and Preston (1952a) have themselves investigated the orientation of structure in the sporangiophore, and believe, on the contrary, that its configuration conforms to the "S" spiral type. Their evidence that this is the case *in the growth zone* is slender, and solely based on the determination of extinction angles in walls showing very weak birefringence. X-ray diffraction methods and electron microscopy as used by them yielded no decisive new information about orientation in the primary wall. In the opinion of the writer, the results of Roelofsen's many-faceted approach to this central issue are a serious blow to the factual foundation of Preston's theory.

In addition to these disputed facts of structure, there are other respects in which Preston's theory is not uniquely supported by evidence at hand. Rotation is a constant accompaniment of elonga-

tion, and both cease together (Oort, 1931; Castle, 1937a); the angle of spiral growth is changed by change of temperature (Castle, 1936b); a torque applied to the growing cell can modify, reversibly, the angle of spiral growth (Castle, 1938b). All these findings are compatible with any theory of the mechanism of spiral growth which assigns an important but modifiable role to the existing wall structure.

The same may be said of the curious fact of brief reversal of the direction of spiral growth when growth of the sporangiophore first recommences after sporangium formation, stage 4a (Castle, 1942; Middlebrook and Preston, 1952b). Preston has stressed the fact that his theory can account for this transitory reversal of the direction of spiralling. The theory does this, formally, by postulating differential changes in the elastic constants of the chitin fibrils. Ingenious as this suggestion is, the reviewer is inclined to think that the phenomenon is intelligible on other grounds, such as the stretching of wall layers which have been laid down during the "rest period" and which may by then have achieved crossed fibrillar orientation (cf. the electron micrographs of Frey-Wyssling and Mühlethaler, 1950).

Preston's formulation furthermore assumes that turgor pressure is constant throughout the entire complex developmental history of the *Phycomyces* sporangiophore. The facts are not surely known, but the velocities of cell-volume increase are so different in the various stages of growth, and the morphologies of the growing regions are so different—apical tip, enlarging sporangium, sub-apical growing zone—that the writer doubts the validity of this assumption. In any inclusive treatment of the whole sequence of developmental changes, events taking place in the mycelium which bear upon growth and development of the sporangiophore (Grehn, 1932) would surely require attention. A striking and neglected fact is that during the swelling of the tip of the sporangiophore to form the sporangium (stage 2), growth of this membrane is simply like the blowing up of a balloon and its fine structure, in surface view under the polarizing microscope, appears to be completely isotropic. Such a radical deviation from conditions of tubular growth and structure prevailing before and after this stage indicates some profound physical or chemical change within the cell which revolutionizes both its wall structure and its mode of growth. In spite of Preston's courage in attacking the problem of spiral growth, it is doubtful whether any unitary theory could actually, rather than formally, give a satisfactory explanation of all the phenomena involved.

Roelofsen, the other principal recent investigator of spiral growth in *Phycomyces*, has developed a more eclectic point of view which assigns a role to structure but which supplements this by supposing that there is a contribution to the orientation of the growth process made by "active intussusception" (Roelofsen, 1950a). By this phrase he denotes a process of wall-building not determined in its direction solely by the mechanical properties of the existing wall. One is reminded of an astute analogy of Oort's (1931), who pointed out that in the construction of a pavement made out of blocks arranged in an oblique or herring-bone pattern, the direction in which the pavement "grows" as it is laid need not coincide with any major axis of the individual blocks. The relevance of such a model to processes in the growing cell wall may be slight, but the point of view is well expressed in it that we cannot safely assume in advance that growth coincides with (or is perpendicular to) any one simple structural axis in the wall.

As has already been mentioned, Roelofsen's studies of wall structure suggest, contrary to Preston, that the average course of chitin fibrils in the primary wall of the sporangiophore (stage 4b) is in a flat, right-handed or "Z" spiral. Such a structure should be more extensible in the direction at right angles to the long axis of the fibrils, just as cellophane sheets extend more readily perpendicular to the main orientation of the cellulose chains. On this basis, the contribution made by the mechanical properties of the cell wall to the orientation of growth should be in the direction of a steep, left-handed or "S" growth spiral, this running approximately at right angles to the flat, right-handed "Z" structural spiral of the wall. It is now well known that the usual spiral axis of growth is indeed such an "S" spiral. Roelofsen (1950a) has further shown that artificially raised pressure in the stage 4b sporangiophore imparts a twist to the cell which is in this same, left-handed direction. Preston, Roelofsen, and the writer would probably all agree, contrary to Frey-Wyssling, that facts of this nature point to *some* real contribution from wall structure to the determination of oriented growth. Whether extension of the cell, either artificially or in the process of growth, is "plastic" or "elastic" or some of each

seems, to the writer, neither possible to state nor important at the present stage of our knowledge.

Roelofsen's evidence that, beyond the influence of oriented wall structure, there is a contribution to spiral growth from a process of active intussusception comes, in part, from a comparison of the angle of naturally-occurring spiral growth in particular cells and the angle of spiralling which the same cells show when plucked and subjected to internal pressure in an "iron lung" device. In this apparatus he finds that the angle of spiral extension is regularly less than the angle of normal spiral growth previously determined. In view of the difficulties attending this extremely delicate experiment, the writer considers it a triumph that Roelofsen was able to measure the relation between elongation and rotation over a range of pressures, and to show that the angle of spiral extension approaches the order of magnitude found in cells growing normally. The fact that all angles found in the cells when artificially inflated were numerically less than the normal angles of growth may or may not be a significant difference. The writer regards this experiment by Roelofsen as exceedingly pertinent, but not decisive in its reported outcome.

The other major evidence for active intussusception cited by Roelofsen lies in a series of measurements on the longitudinal extensibility of the growth zone of artificially inflated sporangiophores, culminating in a plot of the extension of small regions of this zone as a function of their position in the growing region. Topographically, it is found that the extensibility under pressure is greatest at the junction of the sporangiophore with the sporangium, and, passing down the growth zone, extensibility declines along a curve which approaches zero as the bottom of this zone, some 2 mm. below, is reached. When the plotted distribution of longitudinal extensibility along the growth zone is compared with a curve obtained by the writer (Castle, 1937a) for the distribution of increments of growth along the growing zone (a representation of the relative intensities of growth therein), the two curves are found to differ significantly. The growth curve has a maximum; the curve of extensibility does not. From this difference Roelofsen concludes that since extensibility of the wall does not uniformly coincide with where growth occurs, the physical properties of the wall do not solely determine where and how fast growth takes place. The writer assents to this conclusion, but withholds agreement that it necessarily implies that active intussusception contributes to the *orientation* of growth when and where it does occur.

It is noteworthy that Roelofsen, while advocating a determination of spiral growth by more than one agency, has himself supplied important new evidence for a decisive role of wall structure in this process. Artificially raised pressure extends the stage 4b cell along a steep "S" spiral, which is the direction of normal spiral growth; similar pressure applied to the cell during its earlier cessation of growth (stage 3) extends it along a "Z" spiral, which is the direction of growth for an hour or more when it first starts after sporangium formation (stage 4a). It appears inescapable that changed wall structure determines which spiral direction—right or left—growth shall take. In the opinion of the writer, the occurrence of active intussusception is not proved; neither can its occurrence be disproved by the evidence available.

DISCUSSION AND CONCLUSION

Since the lack of success of early attempts to interpret the action of growth hormones of the higher plants through their direct effect on the cell wall, it has become on the whole unfashionable to approach problems of cell growth and morphogenesis in structural terms. Growth is very close to being life itself, with everything included and implied thereby, so that multiple causation of any phenomenon of growth is generally to be anticipated. The writer is convinced, nevertheless, that problems of *orientation* are exceptional, and that the bulk of physical and chemical processes contributing to growth do not confer upon it directional properties. Ultimately these are undeniably contributed by interaction between the given genetic make-up and the environment, but in a more immediate sense definite facts of structure—molecular or gross—must be involved. For example, the growth of limb bones of young mammals is clearly controlled by pituitary secretion, but the shape of the growing bone is, in the immediate sense, certainly more determined by structure already present in the young bone than by the large number of surrounding and contributing chemical circumstances.

We face some such problem in trying to find what factors determine the orientation of the growth process in the sporangiophore of *Phycomyces*. The growing wall is already not randomly structured, its polysaccharide framework

exhibits preferred orientation of the constituent chitin microfibrils, and even this tenuous primary wall consists of more than one layer, with differing average orientation. Nevertheless, the established facts of growth show that the whole growing zone of the cell contributes to growth in an astonishingly regular way, the summated process taking place along a clearly defined helical axis.

The first question which the writer asked himself about these matters, some years ago, was: Is spiral growth strictly structurally determined, like the fixed path of a nut being unscrewed along the thread of a bolt? The answer is: No, because, among other things, the angle of spiral growth is reversibly changed by change of temperature. Such facts suggest that the angle of spiralling is indeed the dynamic resultant of more than one process or force, and this general point of view has been on the whole accepted.

Preston has made a very specific interpretation, in elastic terms, of the possible mechanism of spiral growth, but I doubt whether in its present form this will stand close testing. Roelofsen has contributed important experimental and structural evidence, as well as the suggestion that a process of active intussusception may act together with physical properties of the wall to determine the orientation of growth. As stated above, I am myself not convinced that present evidence demands the existence of this process. The common denominator of agreement among the last three workers would probably be only that the preferred orientation of structure already present in the growing wall is not without a determining effect on the axis of growth.

It must be recalled that the process of sporangium formation involves growth which appears to be truly *un*-oriented. Some influence, therefore, is capable of abolishing the usual tubular mode of enlargement. If this influence is chemical, then a chemical agency can profoundly modify structure and growth, and this would be the nearest approach to a justification of Frey-Wyssling's view that the "protoplasm is sovereign" in these matters. On this chemical hypothesis, it is striking that the contribution made results in the growth of the sporangium membrane being *dis*-oriented (isotropic), rather than positively ordered. One notes with interest, at any rate, that Nature need not always build in terms of tubes and spirals.

There is a distinction between the *mechanism* of oriented growth, as characteristically found in the adult sporangiophore, and the *origin* of spiral growth. The difference lies in how far back one is looking for causation. If we assume the wall of the sporangiophore in stage 4 already to have spirally-wound structure, then it is reasonable to suppose that its mechanical anisotropy conditions, at least in part, the spiral orientation of subsequent growth: this is the generalization apparently subscribed to by Preston, Roelofsen, and the writer, and relates to the problem of more or less immediate mechanism. The problem of origin raises the question: How did this wall structure come to be obliquely oriented in the first place, rather than oriented transversely, axially, or otherwise?

It has been pointed out above that Preston's theory of spiral growth in *Phycomyces* does not face this second question, though in his book (Preston, 1952) he is generally concerned with the problem. Roelofsen (1950a) tentatively suggests that oblique orientation of structure in the tubular cell arises by resolution of two tendencies: a tendency toward deposition of chitin microfibrils transverse to the long axis of the cell, coupled with an axially-directed force, imparted by protoplasmic flow, which may swing fibrils anchored at one end into a resulting oblique orientation.

The writer has earlier (Castle, 1936a) suggested that, because of the peculiar shape of the cell wall in the growing zone of the stage 4 sporangiophore, oblique orientation might arise by a resolution of bending stresses imposed by turgor on structural elements of the wall, in accordance with some "least action" principle. According to this view, spiral growth *originated* from special circumstances arising after sporangium formation, and should not be present in the simple tubular cells of stage 1. Later (Castle, 1942), evidence was given that spiralling of a sort was present in the stage 1 cell, and this appeared fatal for the earlier suggested mode of origin of spiral growth. It is also true that Preston (1952) has called attention to cases of wall structure in the algae where oriented growth would require other modes of interpretation.

Nevertheless, I am not certain that the method of origin of spiral growth I once suggested, and the attention directed toward special events in the life history of the sporangiophore, should be disregarded. The spiralling found in stage 1 cells may be apparent or artificial, rather than real. Evidence for the process comes almost wholly from growth studies depending on the application of a particle, or particles, to the extreme tip of this pointed cell.

In spite of very great precautions, cessation of growth often follows this application, as more recently found also by Middlebrook and Preston (1952a). It is remarkable that it has never been possible, by attaching even one marker as small as a single *Lycopodium* spore, to measure satisfactorily the distribution of growth in the pointed tip of the stage 1 cell, so easy to achieve in the stage 4 cell. All of this points to the extraordinary sensitivity of the stage 1 cell, and to the possibility of producing artifacts of growth and of development by local injury of the wall. Furthermore, the fact that secondary wall structure in stage 1 appears to be just about axially oriented, not spirally, hints that spiral growth in the manifest sense in which it occurs in stage 4 may not be present before sporangium formation. At least these points cry for clarification, for proof or for disproof which will clear the field for a better understanding than we now have of the *origin* of spiral growth. Whether, after all, *Phycomyces* is a fascinating case on the lunatic fringe of botanical particularity, or whether this could equally or better be said of *Valonia*, or *Cladophora*, or *Hydrodictyon*, or of the cotton hair will not be apparent until the process of growth has been adequately investigated in these other forms.

Finally, it is generally admitted that we have no idea why growth of the adult sporangiophore of *Phycomyces* occurs along a *left*-handed rather than a *right*-handed spiral. The preference is not absolute, but it is overwhelming. In the absence of both genetic and causal-mechanical experimentation, it is idle to speculate whether this fact can be traced to chitin-protein complexes, to molecular asymmetry, or to more home-spun developmental occurrences.

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THE CHARACTERISTICS OF RAT POPULATIONS

By DAVID E. DAVIS

Division of Vertebrate Ecology, School of Hygiene and Public Health, The Johns Hopkins University

THE characteristics of a particular group of animals (a population) is the subject of this review. Although biologists have long investigated the characteristics of a group of cells (a metozoan), the study of population is in its infancy. The species used as the experimental animal for this review is the wild Norway or Brown Rat (*Rattus norvegicus*). Millions of domesticated rats of this species have been used for scientific work, but until recently few studies of the life history and ecology of wild rats were conducted. However, because of the economic and epidemiologic importance of the rat, much time and money have been spent in efforts to reduce the numbers of many species of rats. These expenditures, unfortunately, rarely provided data of value for science and also rarely reduced the pest except temporarily.

The subject of the review, the species *Rattus norvegicus*, is the best known of more than 400 named forms in the genus *Rattus*. Some comments will be also included here about the Roof Rat (*R. rattus*), which is represented by numerous subspecies in tropical and subtropical regions. With the exception of the notable studies by McDougall (1944–46) on populations of *R. conatus* in Australia, only miscellaneous observations of the life histories of other species of rats exist. It seems likely, however, that the characteristics of the populations of the various species in the genus *Rattus* differ only in degree and that the characteristics of the populations of Norway Rats will be found largely true for other species, even though there may be great differences in their physical environments.

Since this review is concerned with populations of wild rats, it will exclude a discussion of studies of the individual rat or of domestic rats except when such work clarifies the population phenomena. Thus the vast literature on the anatomy, physiology, genetics, endocrinology, nutrition, human diseases, rat control methods, economic losses, distribution, behavior, and taxonomy will rarely be mentioned.

It seems at the start desirable to indicate briefly the plan of this review. Any population at a given time is the result of the interaction of three general forces. *Reproduction* tends to increase the population, *mortality* tends to decrease it, and *movements* tend to increase it or decrease it depending upon the net result of immigration and emigration. Our present knowledge of the equilibrium of these forces will be reviewed in the first section. The second section will describe the changes in population that result from the interaction of these three primary forces. The third section will describe the action of the environmental factors (habitat, predation, and competition) on the three forces. The inherent capacities of the organism will be mentioned briefly, merely for the sake of completeness. Methods will be discussed where appropriate.

It is also desirable at this point to comment on the conflict between the impossibility of logically dividing the ecosystem (population and its environment) into parts and nevertheless, the necessity of dividing it for analysis and discussion. The above division into forces and factors is artificial because each group interacts with the others. But for an understanding of the population, it is necessary to look at it from different points of view.

Before the detailed data for rat populations are presented, a summary of population theory may be desirable. The simplest situation is a population in a constant environment. Under such circumstances, the population will increase to the capacity of the environment and then remain at that level. At first births are greater than deaths, but at capacity births equal deaths. When the population is below capacity it will increase to capacity along a sigmoid curve. The increase at first is slow, then rapid and then slow again, till at equilibrium it

diminishes to zero. In some cases data are adequate to determine the particular type of sigmoid curve which is applicable, such as the logistic or Gompertz curve. For wild populations the nature of the data rarely justifies detailed curve-fitting.

In nature, a changing environment is obviously more frequent than a constant environment. If the population is far below capacity and hence is increasing, fluctuations in the environment will make little difference in the growth because such fluctuations rarely affect the population. But as the population reaches the equilibrium level, the fluctuations may begin to affect it and to cause changes. Naturally, at the equilibrium level, fluctuations in environmental factors will cause changes in the population number. These general ideas will be tested in this paper by the data about rat populations in nature. The discussion will begin with the analysis of the equilibrium, because that is the simplest case.

The study of animal populations has been pursued from three different aspects by different groups of individuals. An early group of mathematicians and demographers (Verhulst, Pearl, Reed, Volterra) developed mathematical theories of population problems, especially growth, and compared data from human populations to the theories. These mathematical studies generally predicted that, if certain assumptions were true, then a particular result (or set of results) would occur. Since 1930 a number of zoologists in several parts of the world (Gause, Park, Birch, Utida, Stanley) have tested these predictions by raising animals (usually bacteria or insects) in captivity. As would be expected, when the assumptions are fulfilled, the predictions of the mathematicians are verified. In the opinion of some investigators this approach has only limited usefulness because it merely confirms statements about populations in very simple situations and does not reveal new truths apart from those revealed by the mathematicians. Another group has been collecting data on populations, particularly since about 1930 and largely in ignorance of the mathematical and laboratory research. This group of field ecologists has accumulated a large amount of data about reproduction, mortality, and movements, and also about environmental effects on the population. The data are largely empirical, often uncontrolled and frequently undigested. However, the data describe what actually occurs (within limits of error) under the complex conditions of nature, and thus may reveal new truths. Some notable attempts to understand this type of data have been made, especially by Elton and his group at the Bureau of Animal Populations at Oxford. However, most of this work deals with cycles or the practical control of rodents. In the United States the data are widely scattered in a number of journals dealing with natural history, and the research has been directed at mammalogical problems and control methods. The present review selects a small group of species and attempts to merge the data from field observations into a scheme of population relationships and also into the simple mathematical formulations.

I. EQUILIBRIUM

A population that is at equilibrium remains constant for a period of time. Although the individuals themselves are constantly changing, the number is relatively stationary. Before citing the data concerning equilibrium, it is necessary to indicate briefly some of the methods used in estimating rat populations. Methods of estimating the population have been developed for many mammals (Dice, 1941). For rats the methods have been described in some detail (Emlen and Davis, 1949) and will merely be summarized here. (1) The capture and enumeration of all rats in an area is difficult and impractical. (2) The mark-release–recapture method is possible only in certain places. (3) It is possible for an experienced individual to estimate the number of rats in a city block (residential area bounded by streets) by means of signs such as rat feces, trails, runways, holes, food marks, etc. This method has an error of 10 to 20 per cent. While this error may seem large, for present purposes it is satisfactory, since changes in population are the principal concern. This error means, of course, that a factor that affects the population by less than 10 per cent cannot be detected, but this situation is of little concern at the present stage of investigation. This last method is the most frequently used in the present studies.

Emlen and Davis (1948) presented evidence from 4 city blocks in Baltimore that showed a satisfactorily constant population for 10 months. Additional data are available for several additional blocks and a farm. Fig. 1 shows the history of 2 blocks from 1943 to 1950. One block (x), in spite of repeated reductions by poisoning, returned to a level of about 110 rats except in February, 1947, when an unusual snow-fall permitted an increase

in garbage and trash in the yards. The other block (o) tended to return to about 125 rats until June, 1947 (s), when sanitation changed the environment radically. Fig. 2 shows the histories of 5 blocks that were not treated in any way during the time represented. Although the variation in some cases is considerable, it must be remembered that the environment is only relatively constant and that changes do occur in the habitat. Data for additional blocks, presented in Table 1, show stationary populations for two successive years in several cases. Fig. 3 shows the population on a farm. Again the number of rats remains surprisingly constant considering the seasonal changes in farm practices.

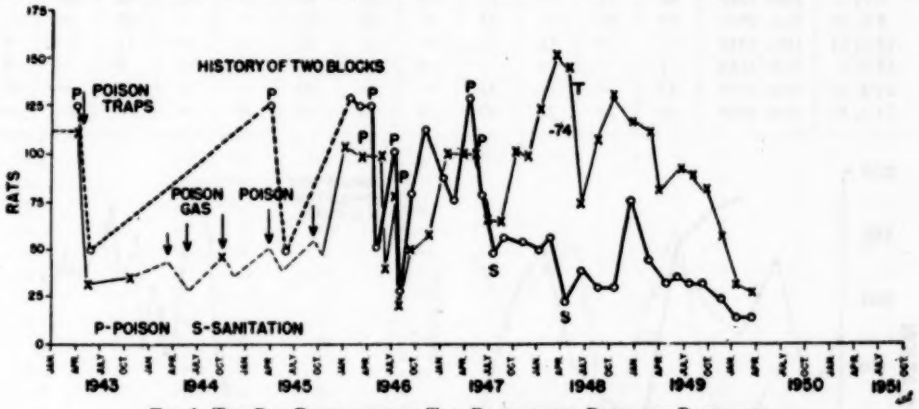


FIG. 1. THE RAT POPULATION IN TWO RESIDENTIAL BLOCKS IN BALTIMORE

Poisoning procedures (P) of various intensities reduced the populations temporarily, but sanitation (S) reduced the population more permanently to a low level. Note that trapping (T) 74 rats in April, 1948, merely interrupted the decline due to changes in habitat.

Dopmeyer (1936) has presented a graph showing a population of rats (mostly *R. hawaiiensis*) nearly constant for more than a year. When the environmental conditions were then changed, the number of rats declined to a very low level.

It is instructive to note the history (Fig. 4) of an increasing population. This population in 1943 was about 100 rats, when they were completely eradicated. Two years later a small number entered the block and within a year increased to 156. Then the population fluctuated about the number of 100 rats, indicating that the capacity in 1950 was about the same as in 1943.

It seems possible to conclude that in nature populations in a relatively constant environment remain relatively stationary in size, or at equilibrium with environmental conditions. This equilibrium is a moving thing, constantly being displaced and then returning to the original state, and there is a constant flow of individuals through the system. Furthermore, even if the total environment (asymptotic conditions) were absolutely constant, there are slight fluctuations due to the variations among individual rats and the fact that rats are not "infinitesimally small" units.

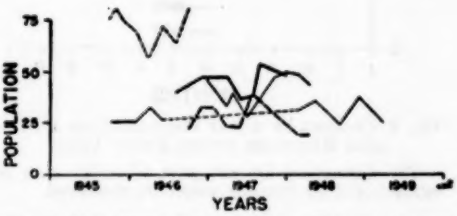


FIG. 2. RAT POPULATION IN FIVE BLOCKS DURING VARIOUS PERIODS OF TIME IN WHICH NO RAT CONTROL WAS ATTEMPTED

The populations fluctuate within fairly narrow limits.

Obviously, when the death of a large rat is compensated for by a birth, the population remains numerically the same, but the mass changes. These slight variations and their compensations result in oscillations about the equilibrium point. Furthermore, in nature the environment is not constant, and hence additional fluctuations develop. Populations are systems that tend to compensate for displacements by returning to

TABLE 1

Number of Rats in Residential Blocks

BLOCK	STARTING DATE	MONTHS SINCE STARTING DATE											
		0	2	4	6	8	10	12	14	16	18	20	22
7-4; 11	June 1950	68	54	70	49	71	57	—	49	—	—	—	—
7-4; 26	May 1950	13	—	—	16	—	—	16	—	—	20	—	—
7-5; 5	May 1950	48	43	38	42	—	—	46	—	—	40	47	48
8-7; 51	June 1949	46	52	—	32	49	50	43	39	43	52	57	—
8-7; 50	Nov. 1949	69	62	—	54	—	67	53	—	—	67	—	—
14-1; 11	Dec. 1948	7	9	11	11	—	—	13	—	—	11	—	9
14-2; 3	Nov. 1948	7	—	—	9	—	—	8	—	—	8	—	8
14-2; 50	Nov. 1949	13	—	—	11	—	—	10	—	—	12	—	14
14-3; 37	Nov. 1949	31	26	27	25	24	31	25	19	—	—	—	—

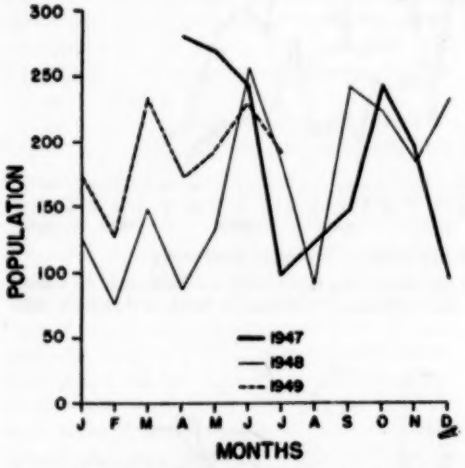


FIG. 3. CHANGES OF A RAT POPULATION ON A FARM NEAR BALTIMORE DURING THREE YEARS

The fluctuations are not great when the error of estimate and the breeding season are considered.

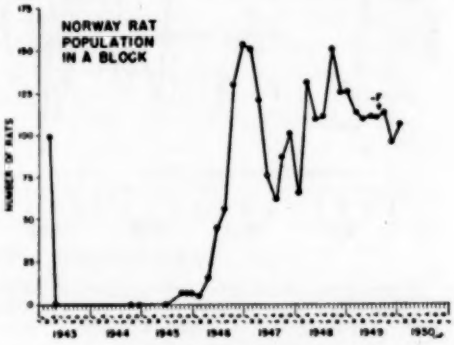


FIG. 4. POPULATION CHANGES IN A RESIDENTIAL BLOCK

Intensive control activities exterminated the rats in May, 1943, but rats returned in late 1945, increased rapidly, declined, and eventually stabilized at approximately the original population. No control whatsoever was done after 1943. The symbol "-F" refers to removal of food for another experiment.

equilibrium, but the combination of constantly changing environmental conditions and the discrete nature of animals result in a population that oscillates about the equilibrium point.

II. CHANGE IN POPULATION

The rate of change of the population at a given time is the result of the interaction of the forces of reproduction, mortality, and movement. While in some cases the + and − components of these forces may be balanced and the sum may equal zero, in most cases the forces are not balanced and hence a change in population occurs. This relation can be simply expressed by the conventional equation $\frac{dN}{dt} = k(B - D)$ (Lotka, 1925, 101), where N is the number of individuals (population), B is births, and D is deaths. The individuals entering or leaving the population through movement may either be included with births or deaths or added as a separate factor. It is obvious that the population will be stationary when $B = D$; be increasing when $B > D$; and be decreasing when $B < D$. The present section will consider the evidence concerning the latter two cases. At present we are not concerned with the factors that determine the values of B and D, but only with their gross value. The discussion of factors is reserved for a later

section, but here it is desirable to note that the same change in population may have different causal factors at different times or places. Knowledge that a change is occurring does not indicate any reason for the change, but merely that the relation of births and deaths has changed.

month, whereas populations reduced less than 50 per cent or more than 90 per cent increased at a slower rate. The curve of increase is sigmoid in form.

Additional evidence concerning the rate of increase has been obtained since Emlen's first experi-

TABLE 2

Rate of Increase of Rat Population

	A	B	C	D	E	F	G	H	I
BLOCK	DATE	ORIGINAL POPULATION	POPULATION AFTER REDUCTION	PERCENTAGE OF ORIGINAL POP.	SUBSEQUENT POPULATION	MONTHS OF INCREASE	NUMERICAL INCREASE OF RATS	PERCENTAGE INCREASE	PERCENTAGE PER MONTH
14-1	18 Sept. 1948	56	3	5	34	8.0	31	55	6.9
7 -4	11 Sept. 1949	128	10	8	68	8.0	58	45	5.6
14-1	60 July 1946	49	6	12	46	6.0	34	67	11.2
11-4	3 July 1946	110	18	16	101	6.0	79	72	12.0
14-3	29 May 1946	90	15	17	58	8.0	43	48	6.0
14-3	14 May 1946	155	28	18	137	6.0	109	70	11.7
14-3	4 May 1946	190	40	21	183	13.0	143	75	5.8
14-1	58 Mar. 1952	40	9	22	32	6.0	26	65	10.9
14-1	32 Dec. 1947	118	28	24	95	10.0	67	57	5.7
7 -5	5 May 1952	48	13	27	48	4.0	35	73	18.3
14-1	18 May 1952	79	21	27	78	7.5	57	72	9.6
11-4	22 July 1946	107	32	29	112	5.0	83	77	15.5
14-3	22 May 1946	110	33	30	122	6.0	89	81	13.5
14-2	20 Mar. 1952	81	25	31	84	7.5	59	73	7.9
14-1	38 Nov. 1951	75	25	33	68	3.0	43	57	19.1
14-3	36 May 1946	197	66	34	149	6.0	83	42	7.0
14-3	42 Mar. 1952	31	11	34	23	4.0	12	39	9.6
14-2	1 Feb. 1952	110	32	34	83	7.5	51	46	6.2
14-3	38 Mar. 1952	32	11	34	29	7.5	18	56	7.5
14-1	32 June 1947	88	35	40	87	2.0	52	59	30.0
14-3	9 May 1946	65	27	42	71	6.0	44	68	11.3
14-2	26 Mar. 1952	67	29	43	63	4.5	34	51	11.3
14-2	22 Mar. 1952	75	34	45	75	4.0	41	55	13.7
11-4	3 Apr. 1948	144	70	49	128	6.0	58	40	6.7
14-3	4 May 1948	163	80	49	103	8.0	23	14	17.5
7 -5	6 Feb. 1952	42	21	50	42	8.0	21	50	6.2
14-2	18 Dec. 1947	110	57	52	104	9.0	47	43	4.8
8 -7	51 Nov. 1948	75	44	59	80	3.0	36	48	12.0
11-4	3 Apr. 1947	92	68	74	108	5.0	40	43	8.7

Increase of Population

The rate of increase of populations of rats living in city blocks in Baltimore was found to be related to the original population in the block, as well as to the numbers remaining after an artificial reduction in numbers (Emlen, Stokes, and Winsor, 1948). Populations reduced by 50 to 90 per cent increased at about 4 per cent per

ment. The usual method was to remove a number of rats from a block and then observe the increase for several months. The fundamental assumption of this type of experiment is that the environment (capacity) of the block remains constant or at least varies less than 10 per cent. Although this assumption was essentially true from 1943–46, since the end of the war extensive improvements in sanitary and housing conditions have lowered the

capacity of many blocks to support rats. Thus rates of increase must be calculated for short periods (less than one year) so that environmental changes will not be excessive. The results for 29 blocks are given in Table 2. In the table (D) is column C divided by column A times 100; (G) is column E minus column C; (H) is column G divided by column B times 100; and (I) is column H divided by column F. By algebraic manipulation it can be shown that I = G/BF. When the values in column I are plotted against the values in column D there is considerable scatter, but a curve is obtained which is in agreement with the predictions that the increase is small for low populations, considerable for medium populations, and low for high populations. A very simple average of the 9 blocks that were reduced to less than 25 per cent of the original populations gives 7.3 per cent per month; for blocks at 25 to 48 per cent of the original, the increase averaged 12.9 per cent per month; for blocks above 48 per cent, the increase was 9.3 per cent per month. This evidence supports the conclusion of Emlen and Davis (1948) that greatly reduced populations increase more slowly than do moderately reduced populations.



A



B

FIG. 5. YARDS IN BALTIMORE BEFORE (A) AND AFTER (B) REHABILITATION

Note the decrease in harborage and food.

The history of the rat population of the block shown in Fig. 4 shows the "momentum effect" which frequently occurs. In recovering, the population goes above the equilibrium value and then drops below it, and may oscillate about that value for some time. This effect is presumably due to some lag in the action of the regulating mechanisms for the population.

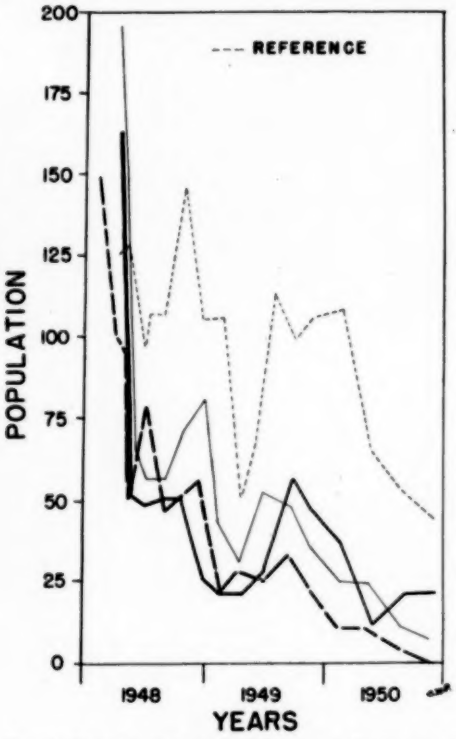


FIG. 6. CHANGES IN RAT POPULATIONS IN REFERENCE BLOCKS AND IN THREE REHABILITATED BLOCKS

The population in the reference block was rather constant until voluntary sanitation in 1949 and especially in 1950 reduced the population. The reduction in the three rehabilitated blocks was rapid and then tapered off to a low level, at which it has remained through 1951.

Decrease of Population

Thus far we have considered a population that was purposefully reduced below the capacity of the

area and then permitted to increase. We next consider the decrease in population in a block the capacity of which has been lowered. For best results it would be desirable to lower the capacity instantaneously, but of course such conditions can rarely be obtained with natural populations. However, in cooperation with officials of the Baltimore City Health Department, it was possible to study the rat population in city blocks that were being rehabilitated. Rehabilitation consists of a radical improvement for people of the housing and sanitation conditions in slum blocks. An inspector serves notices to tenants and landlords in the entire block to remove junk, tear down fences, cement basement floors, get garbage cans, etc. Although the environmental changes are not instantaneous, within a month extensive alterations have occurred (Fig. 5). The decrease in rat population for 3 rehabilitated blocks is shown in Fig. 6. The reference block had a constant population during the period of rehabilitation in adjacent blocks, but then fluctuated from 110 to 50 to 90 rats because of changes in its sanitary conditions. Additional evidence may be obtained from blocks that are inspected by sanitary police (Fig. 7). Their program of sanitation is not as drastic as rehabilitation, and the results are less rapid.

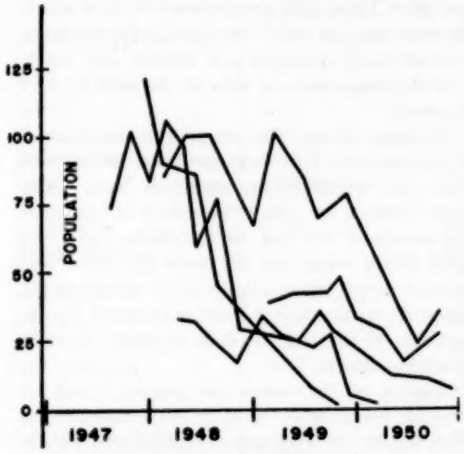


FIG. 7. POPULATION CHANGES IN CERTAIN RESIDENTIAL BLOCKS

These received less drastic enforcement of sanitation in early 1949. Note that enforcement sometimes occurred long after population had naturally declined.

The results of this study of the increase (see Table 2 and Fig. 4) and decrease (Fig. 6) of populations of a wild mammal are considered to agree with the important characteristics of the logistic curve of Verhulst, Pearl, and Reed. Lotka (1925: 66) gives a full discussion of the curves, which are reproduced in Fig. 8. The lower curve represents the approach of a low population to capacity and corresponds to the data for increasing populations. The upper curve refers to populations decreasing to the asymptote. The capacity is obviously the asymptote or equilibrium attained by the population. It must be remembered that

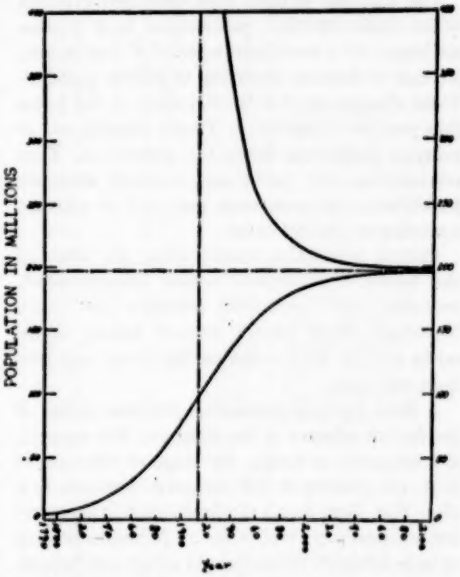


FIG. 8. LOGISTIC CURVE DESCRIBING THE INCREASE IN POPULATION OF THE UNITED STATES AND THE THEORETICAL DECLINE OF A POPULATION TO AN ASYMPTOTIC VALUE

From Lotka (1925).

nothing is explained by stating that the data agree with a particular type (logistic) of equation because the mechanisms are not described. However, the description of population changes is simplified, and cautious predictions are possible. Actually all we have is a "rat curve" which happens to be similar in shape of the "human curve." The reasons for the shapes need to be determined by the ecologists.

The above discussion has assumed the presence of a constant environment or at least the occurrence of only minor changes, except those planned as a part of the experiment. Great changes in rat

populations may occur naturally as the result of radical environmental changes. The variation in number of rats reported by Mohr (1947) are presumably due to changes in agricultural practices in the rural areas of Illinois. In these cases we may think of the population as being practically asymptotic (slight lag) at all times but with the asymptote fluctuating drastically and rapidly.

III. POPULATION FORCES

The previous sections have described evidence which indicates that populations may remain stationary for a considerable period of time or may increase or decrease according to definite patterns. These changes are due to alterations in the forces that produce a population. Forces actually add or subtract individuals from the population. Thus *reproduction* adds individuals, *morality* subtracts individuals, and *movements* may add or subtract according to the net value.

Certain population factors affect the value of the forces. The *physical habitat* (environment), *predation*, and *competition* influence the forces. Naturally, these factors interact among themselves and by their action on the forces may produce reactions.

A third aspect of population problems is that of the factors inherent in the organism. For example, the resistance to toxins, the range of tolerance of heat, etc., belong in this category. Although it is clear that these forces are fundamental, here they are practically omitted from the discussion because so little is known about them in nature and because in most cases the investigations deal with populations whose individuals are considered to be practically identical in these respects. Our present knowledge of the population forces will be considered next.

Reproduction

The term reproduction normally refers to the process associated with birth, but also to the number of young added to the population. However, the latter use is unsatisfactory because the number added to the population is merely the result of a series of mortalities occurring after birth. Strictly speaking, reproduction should refer to the number of ova ovulated or some such basic number. In practice these data are unobtainable in quantity and are meaningless to the population because mortality starts right away. The number of rats weaned (which is of value for population studies) is what remains after intra-uterine, parturitional, and suckling mortality. To indicate the effect on the population, the less familiar term "recruitment" is far superior to "reproduction."

Buxton (1936) summarized the meager knowledge concerning breeding rates of rats in various parts of the world and also repeated the plea for more rational recording of data from the thousands of rats killed during control procedures. Since that time much material has been accumulated and will be discussed under the topics: breeding season, pregnancy rate, suckling rate, and young per year. These data are presented in some detail because they are widely scattered in the literature and are rarely accessible, and because they represent the largest mass of data of the kind for any mammal.

Breeding Season. The extent of recruitment in a year naturally depends in part upon the length of time the species can reproduce. Rats, unlike most rodents, are able to reproduce in nature at all seasons of the year. In Baltimore, Davis and Hall (1948) found that the males had sperm and mature secondary sex-organs at all seasons of the year. At no season was there evidence of the regression of the testes that is regularly found in cricetine rodents.

Studies of the female are usually based on "visible pregnancies," a term which refers to the fact that the embryos may be seen macroscopically in the uterus for about 18 of the 25 days of pregnancy. The prevalence of "visible" pregnancy is satisfactory for seasonal comparisons since the above relation does not change, but this prevalence is of course only about eighteen twenty-fifths (72%) of the true prevalence of pregnancy. Unless otherwise specified the following reports are based on visible pregnancies. The data graphed in Fig. 10 from a number of places refer to the percentage of adult females that had visible embryos, except for England (urban) 1941–42. The references to the definition of "adult" and to total number of rats may be found in Tables 3A and 3B.

Davis and Hall (1951) showed that, although some pregnant females were found at all seasons of the year, in Baltimore warehouses there was a bimodal curve for the prevalence of pregnancy, The two peaks, which occurred about June and October, resulted from the fact that, although big females bred at a uniform rate, the small rats became pregnant in numbers only

TABLE 3A

Reproductive Rates of Norway Rats

LOCALITY	CATEGORY	FEMALE RATS	PER CENT PREGNANT	EMBRYOS PER PREG. FEMALE	INCIDENCE OF PREGNANCY	REFERENCE
Baltimore warehouses 1946	perf. vag.[1]	437	23.6	9.4	4.8	Davis & Hall (1951)
	10–12 nip.[2]	317	32.9	10.0	6.6	
	over 199 mm.	196	40.3	9.8	8.3	
Baltimore farm 1946–47	perf. vag.	312	21.1	8.2	3.9	Davis (1951a)
	10–12 nip.	178	33.9	8.2	6.3	
Baltimore population 1947–49	stationary	442	18.6	10.3	3.8	Davis (1951d)
	increasing	263	29.8	10.3	6.1	
	decreasing	162	30.9	9.9	6.3	
Baltimore outdoors 1943–45	perf. vag.	1481	23.3	9.9	4.7	Emlen, unpub.
	over 199 mm.	920	27.2	10.1	5.5	
	over 249 mm.	203	27.9	11.2	5.7	
San Antonio, Texas farm	over 130 mm.	610	13.6	7.9	2.7	
	over 180 mm.	379	17.0	8.3	3.4	Davis, unpub.
	over 200 mm.	199	21.1	8.2	4.3	
Norfolk	adult	620	34.1	—	6.9	Hasseltine (1929)
Urban	12–14 inches	6220	3.9	—	0.8	
San Francisco	over 14 in.	12962	20.7	8.9	4.2	Storer & Davis (1953)
Bombay	over 100 g.	27278	15.1	8.1	3.1	India Plague Comm. (1907)
England	adults	660	22.8	7.5	4.6	Perry (1945)
England farms	rick	1180	30.0	8.9	6.0	Venables (1942)
	non-rick	542	16.5	9.3	3.3	Leslie (1952)
Germany	over 163 mm.	1824	17.7	—	3.6	Becker, (1951)
Germany	over 160 mm.	620	31.4	8.7	6.4	Peters, (1948)
Boston	adult females	?	7.0	—	1.4	Eaton, Stirret (1928)
San Diego 1934	18–23 inches	791	19.0	—	—	Davis, unpub.
	24 inches	154	32.4	—	—	
	all females	945	21.2	—	—	
Dothan, Ala. 1933–34	21–23 inches	869	10.1	—	2.0	Davis, unpub.
	24 inches	534	12.5	—	2.5	
	all females	1403	10.7	8.4	2.2	
Savannah, Ga. 1932–33	18–20 inches	559	6.2	8.0	1.3	Davis, unpub.
	21–23 inches	849	14.9	8.2	3.0	
	24 inches	434	20.7	8.7	4.2	
	all females	1842	13.7	8.4	2.8	
Jacksonville 1934	18 inches	2015	14.3	8.9	2.9	Davis, unpub.
Georgia 1947–49	perf. vag.	2202	18.9	9.2	3.8	Morlan (1952)
	LACTATION RATES					
Baltimore warehouses 1946	perf. vag.	434	34.5[4]	3.5[5]	—	Davis & Hall (1951)
	10–12 nip.	305	45.9	4.6	—	
	over 199 mm.	199	55.9	5.6	—	
Baltimore farm 1946–47	perf. vag.	307	22.0	2.2	—	Davis (1951a)
	10–12 nip.	179	38.0	3.8	—	
Baltimore 1947–49 (population)	stationary	439	43.0	4.3		Davis (1951d)
	increasing	254	42.4	4.2	—	
	decreasing	162	39.9	4.0	—	

[1] Perf. vag. means that the vaginal orifice was perforated.

[2] 10–12 nip. means that the rats had 10 to 12 nipples.

[3] Values differ from the reference because of standardizing for months.

[4] This column gives percentage lactating.

[5] This column gives incidence of lactation.

during those two seasons (Fig. 9). In another study Davis (1951a) compared the breeding season of rats captured on a farm with that of rats captured outdoors in residential parts of Baltimore. The curves were similar (Fig. 9) although the peak of pregnancy was earlier on the farm than in the city. An analysis of lactation of 1874 mature female rats (viz., rats with a perforated vaginal orifice) caught on this farm during 1949–51 showed a bimodal curve, with the highest peak in the spring and a secondary peak in the early fall (Davis, unpub.). Rats caught in 1943–45 in the urban residential areas mentioned above showed a definite low in the winter (Fig. 9), and in contrast to other studies, there was no secondary peak in the fall.

In the other parts of the United States a bimodal curve has been found. McCoy (1912) found no evidence of seasonal changes in pregnancy rates for rats in San Francisco, but his data were calculated on the basis of the percentage of all females found to be pregnant and thus cannot be analyzed now. Davis (1948a) found that Norway Rats captured indoors in San Antonio had a peak in pregnancy only in the spring (Fig. 10). Hasseltine (1929) found a bimodal curve of pregnancy for Norway Rats in Norfolk, with peaks in the spring (Fig. 10) and fall. Storer and Davis (1953) found in a very large sample of Norway Rats from San Francisco that there was a peak in May and September (Fig. 10). Morland, Utterback, and Dent (1952) found a bimodal curve in Georgia.

Only a few reports from other parts of the world give data in adequate form for analysis. The India Plague Commission (1907) published excellent data for Bombay that showed rather constant pregnancy rates for Norway Rats, but with a statistically significant low in January and a peak in March (Fig. 10). Perry (1945) found considerable seasonal variation among urban Norway Rats, with peaks in May and October and an unexplained high value in January (Fig. 10). In England, Venables and Leslie (1942) found a bimodal curve for Norway Rats living in corn ricks with peaks in October and May (Fig. 10). Leslie, Venables, and Venables (1952) revised the data and confirmed the bimodality for ricks and also for "non-rick" rats. Becker (unpub.) found

TABLE 3B

Reproductive Rates of Roof Rats

LOCALITY	CATEGORY	FEMALE RATS	PER CENT PREGNANT	p^{2} FEMALE	INCIDENCE OF PREGNANCY	REFERENCE
San Antonio	over 120 mm.	917	18.4	7.2	3.7	Davis, unpub.
	over 160 mm.	470	28.6	7.2	5.9	
	over 180 mm.	227	32.1	7.3	6.5	
Thomasville	over 140 mm.	279	26.5	5.8	5.4	Davis, unpub.
Tampa	perf. vag.	275	30.0	6.4	6.1	Davis, unpub.
San Francisco	over 15 in.	3633	26.5	7.4	5.2	Storer & Davis, unpub.
London	c. l.[1] in ovary	598	31.6	6.5	6.4	Watson (1950)
London (ships)	c. l. in ovary	315	37.1	7.5	7.5	Watson (1950)
Cyprus	c. l. in ovary	566	14.6	6.0	3.0	Watson (1950)
India	50 g.	13326	22.6	5.9	4.6	White (1914)
Bengal	70 g.	2041	29.4	—	6.0	Plague Comm. (1911)
Bombay, India	70 g.	16817	25.7	—	5.2	Plague Comm. (1908)
Belgaum, India	70 g.	11925	43.3	5.3	8.8	Plague Comm. (1910a)
Punjab, India	70 g.	2820	36.3	—	7.4	Plague Comm. (1908)
Poona, India	70 g.	13693	38.6	—	7.8	Plague Comm. (1910b)
Egypt	65 g.	9788	33.3	—	6.7	Petrie & Tood (1923)
San Diego	15 in.	244	15.3	—	—	Davis, unpub.
Honolulu	15 in.	473	36.2	6.3	6.4	Davis, unpub.
Georgia, 1947–49	perf. vagina	4978	25.4	5.6	5.1	Morlan (1952)
Cyprus	c. l. in ovary	572	12.9	6.1	2.6	Watson (1951)

[1] Corpora lutea present.

a bimodal curve in Berlin, but Peters (1948) found unimodal curve with a peak in May in Stuttgart (Fig. 10).

Data for Roof Rats are available from a number of places (Table 3B). In Tampa there was a definite peak in spring, but in San Francisco no seasonal

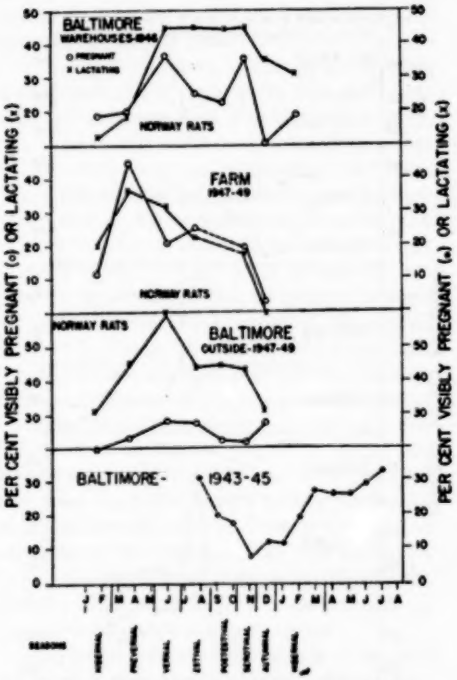


FIG. 9. BREEDING SEASON OF NORWAY RATS AT BALTIMORE

Rats from warehouses show a bimodal curve of pregnancy but a unimodal curve of lactation. Rats captured on a farm (1947–49) show a unimodal curve, although data were too meager to be plotted (dotted portion of curve) for the postestival season. Rats captured in residential areas (1947–49) show a maximum in the vernal season and in the autumnal. Lactation shows a peak in spring. Rats caught in 1943–45 in the same area showed a clear minimum in the winter. (See Table 3A for references and for the number of rats in each sample.)

variation was obvious (Fig. 11). In the docks and warehouses of the Port of London a peak in spring is clear, but on the ships (Fig. 11) the spring peak is not certain (Watson, 1950, p. 5). In Cyprus (Watson, 1950) there is probably a bimodal curve (Fig. 11). Davis (1947) found a suggestion of bimodality in rural areas of Texas although later (1948a) he found a unimodal curve for urban rats in San Antonio (Fig. 11). Morlan, Utterback, and

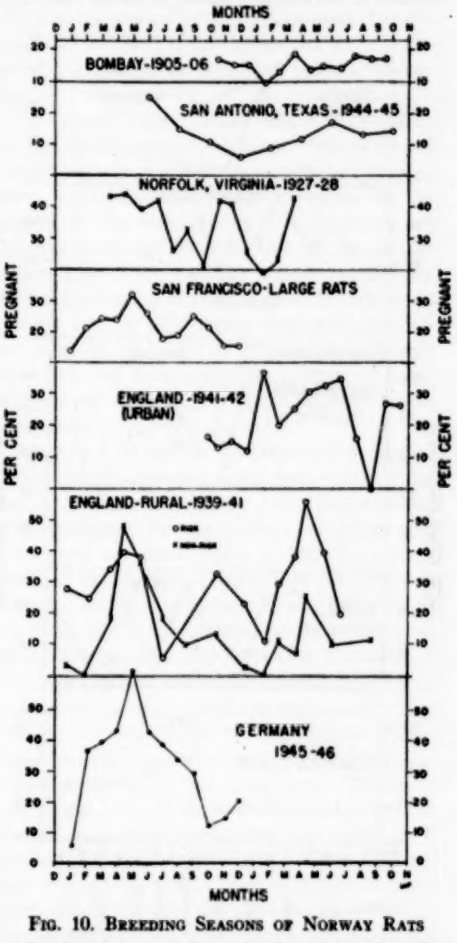


FIG. 10. BREEDING SEASONS OF NORWAY RATS

Bombay has a minimum in the winter time. San Antonio also shows a minimum in winter. Norfolk shows peaks in the fall and spring, as does San Francisco. The England (urban) data are based on true (not visible) pregnancy and show two peaks, with an unexplained high value in January. The England (rural) data show a bimodal curve for the rats found in the fields. The rats from Germany show an amazingly high pregnancy rate in spring.

Dent (1952) found bimodality in rural rats in Georgia.

A wealth of data is available in the reports of the Indian Plague Commission (1907, 1908, 1910a,

1910b, 1911) for Roof Rats. The curves for five places (Fig. 12) are generally unimodal, with minima in the cold dry season, although data from Belgaum and the Punjab showed additional peaks in the monsoon season. Data from Egypt (Petrie and Todd, 1923) show a definite season of low reproduction in the winter. Even on the Hawaiian islands, which have a relatively uniform climate, Eskey (1934) found a pregnancy rate of 0.25 in August, in contrast to a prevalence from November to January of about 0.04. Watson (1951, p. 14) presents a bimodal curve for Roof Rats in Cyprus.

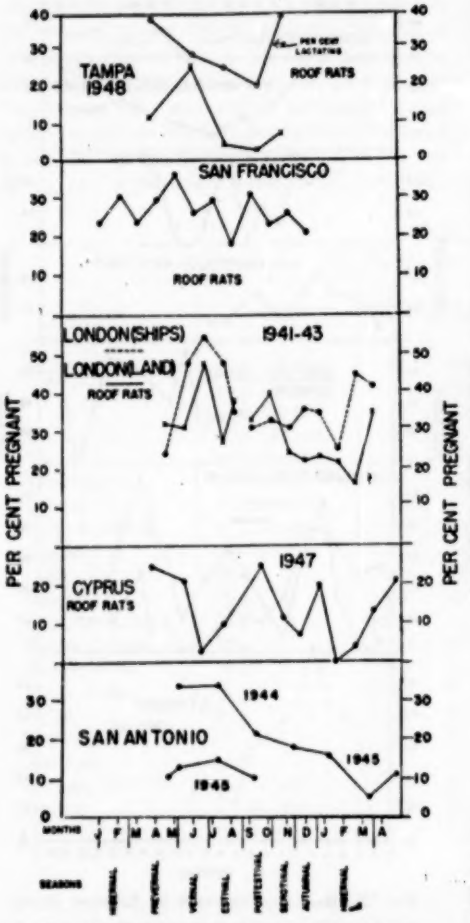


FIG. 11. BREEDING SEASONS OF ROOF RATS

A small collection of Roof Rats from Tampa, Florida, shows a peak in the spring. Rats from San Francisco show no regular seasonal changes. Rats from both ships and docks at London show unimodal curves with maxima in the spring. Rats from Cyprus have a bimodal curve with a somewhat aberrant peak in January. Roof Rats from San Antonio, Texas, showed maxima in early summer and a minimum in early spring. The curves all represent the percentage of visibly pregnant females.

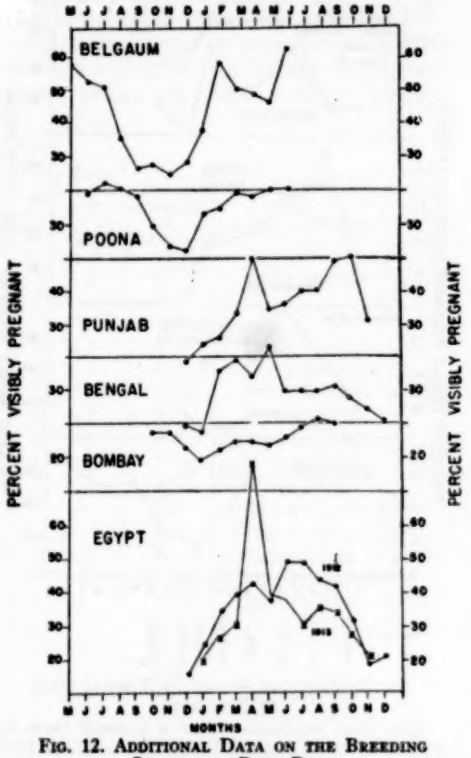


FIG. 12. ADDITIONAL DATA ON THE BREEDING SEASONS OF ROOF RATS

Curves for Roof Rats from five places in India, plotted from data published by the Plague Commission, show rather similar seasonal changes. The minimum is in the cold dry season (about October to January), and the maximum in the hot dry season (about February to June). A secondary peak is present in the Punjab data in the monsoon season. Data for two years from Egypt differ in date of the summer maximum but agree upon a winter minimum.

For Dakar, Cazanove (1931) gives data for a very large series of rats, but unfortunately data are lacking for February and March. The data indicate a unimodal curve for three species of rats, but are based on all females and are hence open to various interpretations.

These studies, which appear to be the only ones

giving data in a form suitable for analysis, show that Norway Rats and Roof Rats produce young throughout the year and at least in some cases have two periods of high pregnancy rates. The data are not analyzed in detail for relation to climate because adequate microclimatic data are lacking in all cases. In general, there is a minimum in the cold season, and there may be another minimum in the hot season.

Prevalence of Pregnancy. Although the breeding season is indicated in terms of the changes in pregnancy rate, the rate itself is of importance in the force of reproduction. The data concerning prevalence of pregnancy are summarized in Tables 3A and 3B only for the reports that are based on mature females, since reports based on all females are of little value. It should be noted that, except for Perry's data from England, prevalences are based on the percentage that are pregnant according to macroscopic examination of the uterus. The data in Tables 3A and 3B are self-explanatory. In addition some other reports are available. Harrison (1951, p. 685) presents data for the prevalence of visible pregnancy for several forms of Roof Rats in Malaya. For *R. r. diardi*, the prevalence was 0.263 for 1018 females that weighed more than the mean weight at first pregnancy (which is somewhat higher than the weight at perforation of the vaginal orifice). The prevalence for *R. r. jalorensis* from three areas differed considerably (0.15, 0.23, 0.43), but the numbers of rats were small except for the first area.

A positive correlation between size of rat and prevalence of pregnancy has been found for Norway Rats in England (Venables and Leslie, 1942; Leslie, Venables, and Venables, 1952); Perry, 1945). In Berlin Becker (1951) found a similar correlation. Davis and Hall (1951) found that the prevalence of visible pregnancy varied in Baltimore according to the size of the rat. For all mature females (rats with a perforated vaginal orifice), the prevalence was 0.236. For medium and large-sized rats (rats with 10–12 nipples) the prevalence was 0.329. For large rats (over 200 mm. in body length) the prevalence was 0.403. A similar relationship was found for Norway Rats caught outdoors in residential areas of Baltimore and on a farm (Davis, 1951a), Norway Rats and Roof Rats in San Antonio (Davis, 1948a), and for Roof Rats on farms in Texas (Davis, 1947). A similar correlation was found for Roof Rats in India (White, 1914), London (Watson, 1950), Cyprus (Watson, 1950, 1951), and Georgia (Table 4) (Morlan, Utterback, and Dent, 1952). Harrison (1951b, p. 686) found that prevalence increased with size for several forms of Roof Rats, but decreased at the largest size groups for *R. r. diardi* and *R. exulans*. The biological meaning is not clear.

The data in Tables 3A and 3B are calculated in groups that represent different definitions of "adult" because of the significance, to be discussed later, of production of young. However, for the analysis of size relationships it is better to use exclusive groupings. Thus the data for the relation of pregnancy to size for San Antonio are: 5.6 per cent of 231 females that were 130–179 mm. long; 13.9 per cent of 180 females that were 180–199 mm. long; 21.1 per cent of 199 females that were more than 199 mm. long. The increase of pregnancy with size is very obvious from these calculations.

Incidence of Pregnancy. In the study of populations a statistic of fundamental importance is the number of litters weaned per year. This number, when multiplied by the number of young per litter, gives the total young weaned in a year. However, the number of litters born per year can be approximated (Emlen and Davis, 1948; Davis and Hall, 1951) by determining the number of pregnancies per year and estimating the number actually born. The annual incidence of pregnancy derived from such calculations for the available data are given in Tables 3A and 3B. The data are standardized to compensate for seasonal differences in prevalence of pregnancy as follows: The percentages pregnant for all months (or seasons) were summed and then divided by the number of months. This method essentially assumes that an equal number of rats (100) was caught in each month. These standardized percentages are necessary for comparisons of incidences of pregnancy from place to place. The data, however, are not always standardized to account for differences in size of rat because of the lack of detailed information in many cases. The difference between crude percentages and those standardized for size are probably not great. For example, Venables and Leslie (1942, p. 58) give in their Table 5 for the rick rats a standardized percentage of pregnancy that gives a weighted (for months) mean of 30.0 per cent for 1939–41. When the same data are used to calculate a weighted mean without standardizing for size, the result is 29.1 per cent. Errors of

this magnitude are not important when differences of habitat, trapping, diagnosis of pregnancy, etc., are considered.

The uniformity of the incidence in various parts of the world is striking. The modern data (Tables 3A and 3B) that can be analyzed by size of rat give values very close to 5 litters per year for Baltimore (indoors and outdoors), Texas, and England (farms and urban). The incidence of pregnancy on a farm near Baltimore was somewhat lower, possibly due to a deficient diet (Davis, 1949b). A comparison in Baltimore of rats from populations that were stationary, increasing, or decreasing showed that the stationary population had a low rate (3.8), the increasing population had a high rate (6.1), and surprisingly, the decreasing population had a high rate (6.3). The data for Boston, Bombay, and Norfolk vary but probably represent differences in definition of the "adult" rat. In Bombay the 100 g. limit probably includes many young rats and thereby gives a low prevalence. For Norfolk there is no definition of "adult" but the large value of the prevalence reported suggests that only rather large rats were included. A similar explanation may apply to Boston. It should be noted that Eaton and Stirrett (1928) used 16 days instead of 18 days for the time embryos are visible and hence obtained a value of 3 to 4 litters per year. Leslie, Venables, and Venables (1952) published a very detailed analysis of their 1939 data. After standardizing for size and season they get an incidence of pregnancy of 4.8 for rick rats and 3.1 for non-rick rats.

Roof rats from a variety of places (Table 3B) show considerable uniformity in the incidence of pregnancy. The values usually are about 5 litters per year, much of the variation being due to the definition of an adult.

Number of Young per Year. The number of young born per year may be obtained by multiplying the incidence of parturition by the number of young born in each litter. Leslie, Venables, and Venables (1952) examined nests from ricks and found about 7.3 young per nest. This is a decrease of 18 per cent from the mean number of embryos (8.9). It is possible that some young were not found, so that the real decrease would be less than indicated. These young presumably had suffered some loss since birth, so the number born would be a little higher than 7.3, perhaps 7.5.

However, in general the number of young and the number of parturitions can rarely be obtained. Hence, the number of embryos per pregnant female and the incidence of pregnancy are used as an approximation to the number of young per year. This value, of course, neglects some intra-uterine mortality. The work of Perry (1945) on Norway Rats indicates that there is a loss of about 1.6 embryos during visible pregnancy. However, Hall and Davis (1950) found negligible intra-uterine mortality after implantation. Watson (1951, p. 18) found in Roof Rats a loss of about 1 embryo during the implanted phase, and Harrison (1951, p. 690) found a similar loss for several Malayan rats and suggested that the number at birth is 92 per cent of the mean embryo count. To correct partially for intra-uterine loss, it is possible (Emlen and Davis, 1948) to consider only the rats with embryos near term, in order to get an approximate litter-size; in this case the number of embryos per pregnant female was 9.9 and the number of embryos per pregnant female with large embryos was 9.0. The number of embryos per year per female obtained by multiplying the incidence of pregnancy by the mean number of embryos, strictly speaking, applies to the 16th day of pregnancy, since the average values of incidence and the numbers of embryos are obtained from rats observed between the 7th and 25th day of pregnancy. The number of young actually born per female per year will be about 10 per cent less, since there is a loss of about one embryo from the 16th day to the 25th day and apparently the loss of entire litters is small during this period (Perry, 1945).

The number of young born per year can be approximated from Tables 3A and 3B. In addition to the tabulated data, figures for Malayan rats are available (Harrison, 1951, p. 688). For 268 *R. r. diardii* the mean was 5.7. The mean number of embryos for three populations of *R. r. jalorensis* was 3.5, 4.8, and 5.8, values which are a little less than those for urban rats given in Table 3B. The number of young per year for *R. r. diardii* is 27, and the other forms varied considerably according to place. From the population viewpoint, however, the number born per year is not of great importance because of the unknown but probably great post-parturitional mortality. The figures for the number born per year per female are merely a beginning in the analysis of reproductive rates and will require many additions before generalizations can be attempted.

The number of embryos increases somewhat

with the size of the female. Examples are given in Table 3A in the column for the number of embryos. For the rats from Baltimore warehouses, Baltimore indoors, and San Antonio, the number of embryos is smallest in the smallest size-category of rats. Table 4 gives detailed data for Georgia. Harrison found an increase of embryos with size of rat for *R. r. diardii* and *R. exulans*.

Leslie, Venables, and Venables (1952) found the same relation and stated that it was necessary to correct for size composition of sample when comparing places. Because the increase with size is small and because the small-sized rats comprise a low proportion of the pregnancies, no great error is made in neglecting this relationship and simply using crude averages for comparison of reproductive rates in different areas. The number of embryos changes little with season (Davis and Hall, 1951; Morlan, Utterback, and Dent, 1952).

Incidence of Lactation. The number of times during a year that a female suckles young may be obtained (Davis and Hall, 1951) from the prevalence of lactation. The prevalence of lactation must be standardized to correct for seasonal differences in the number of rats captured. As in the case of pregnancies, the sum of the monthly (or seasonal) percentages is divided by the number of months (or seasons) to give the standardized means in Table 3A and 3B. The range of the incidences can also be calculated (Davis and Hall, 1951) to give some idea of the variability. It was concluded (Davis and Hall, 1951) that the large rats have a higher incidence of lactation (see Table 3A) and also (Davis, 1951d) that stationary, increasing, and decreasing populations have similar incidences of lactation.

It is obvious that the incidence of lactation must be larger than the incidence of weaning, since some entire litters are lost during suckling and also some individuals may be lost from a litter. It is perhaps permissible to speculate on the number of young weaned by assuming a mortality of 0.5 total litters and of 2 young per litter for the period from the midpoint of suckling till weaning. For rats with a perforate vaginal orifice from Baltimore warehouses the incidence of weaning, on these assumptions, would be 3.0 and the number of young would be 7.4, thus giving a value of about 22 young rats weaned by a female during a year. Unfortunately, better data are not yet available.

Another aspect of the reproductive rate is the age at which individuals become sexually mature. The chronological age is difficult to determine, but Leslie, Perry, and Watson (1946) applied mathematical procedures to determine the size (weight or length) at which 50 per cent of the individuals attain maturity. Maturity, of course, can be defined in various ways. Leslie, Perry, and Watson (1946) used ovulation as the standard. Davis (1949a) and Davis and Hall (1951) used a similar method to determine the 50 per cent point for various definitions of maturity, while Davis and Emlen (1948) determined the size at which 50 per cent of the rats were parous. Tables 5A and 5B show the results of these analyses. Unfortunately, the older literature contains only vague statements about the size at sexual maturity, based on casual observations of individuals and lacking a definition of maturity. The size at sexual maturity will depend naturally upon the size of rats in the population. Rats in a population whose rats are large, on the average, will attain maturity at a larger size than individuals in a population whose rats are small. Hence, Davis (1949a) compared the size at maturity by calculating the ratio between size at which 50 per cent of the individuals reach maturity and the mean size of the rats in the population. These ratios really standardize the

TABLE 4

Relation of Size to Pregnancy and Number of Embryos
(Morland, Utterback and Dent, 1950)

	ROOF RATS			NORWAY RATS		
Mid-point length	Mature females[1]	Per cent pregnant	Mean no. of embryos	Mature females[1]	Per cent pregnant	Mean no. of embryos
135	292	1.7	4.6	—	—	—
145	487	6.4	4.7	—	—	—
155	775	15.2	5.1	—	—	—
165	1022	30.3	5.4	—	—	—
175	1135	35.4	5.6	186	1.6	7.3
185	834	37.7	6.0	195	8.7	7.1
195	275	33.1	6.3	239	16.3	7.3
205	39	35.9	6.1	262	26.7	8.3
215	2	50.0	8.0	294	22.1	9.1
225	2	0	—	289	29.8	9.7
235	2	50.0	6.0	211	29.9	10.0
245	—	—	—	140	32.2	10.8
255	—	—	—	51	33.3	10.4
265	—	—	—	17	47.1	11.3
275	—	—	—	3	0	0

[1] Mature means that the vaginal orifice was perforated.

populations for comparison. A high ratio means that the rats are relatively large at attainment of the character.

The data in Table 5A, though meager, do indicate a uniformity for Baltimore rats that live under similar conditions. Perhaps most interesting is the similarity of the 50 per cent points for ovulation from 4 samples in England and from the Baltimore sample.

A consideration of the ratios in Table 5A shows some differences among localities. The farm rats are relatively heavy at the time of descent of the testes in the males and perhaps at perforation of the vaginal orifice in the females. But the lengths are about the same for these characters. These data are included principally to suggest a method for comparison of size at sexual maturity and because they indicate the magnitude of variations from place to place when, as on the farm (Davis, 1949b), the diet is obviously deficient.

TABLE 5A

Size of Norway Rats at Sexual Maturity

PLACE	HABITAT	50% POINT		RATIO		REFERENCE
		g.	mm.	g.	mm.	
Scrotal Testes						
Baltimore	farm	136	—	.68	—	Davis, 1949a
Baltimore	farm	157	165	.91	.96	Davis, 1951a
Baltimore	residential	119	171	.45	.84	Emlen, unpub.
Baltimore	residential	109	155	.34	.76	Davis, 1951a
Baltimore	warehouses	105	141	.45	.81	Davis and Hall, 1949
England	urban	190	—	—	—	Leslie et al., 1946
Germany	urban	93	153	.69	.92	Becker, 19[illegible]1
Perforated Vaginal Orifice						
Baltimore	farm	88	—	.50	—	Davis, 1949a
	farm	72	134	.42	.78	Davis, 1951a
	residential	105	154	.39	.75	Emlen, unpub.
	residential	123	150	.39	.74	Davis, 1951a
	warehouses	102	143	.53	.85	Davis and Hall, 1951
Germany	urban	103	159	.81	.97	Becker, unpub.
Ovulation						
England	urban	145	—	—	—	Leslie, et al., 1946
	urban	146	—	—	—	Leslie, et al., 1946
	urban	113	—	—	—	Leslie, et al., 1946
	urban	144	—	—	—	Leslie, et al., 1946
Baltimore	warhouses	153	144	.79	.86	Davis and Hall, 1951
Placental Scars						
Baltimore	residential	242	224	.93	.95	Davis and Emlen, 1948
	residential	305	212	1.07	1.07	Davis, 1951a
	warehouses	318	216	1.64	1.28	Davis and Hall, 1951
	farm	*	*	—	—	Davis, 1951a
San Antonio	urban	178	—	1.21	—	Davis and Emlen, 1948

* Did not reach 50% with scars.

It is also possible to compare the size at first parturition by determining the length or weight at which 50 per cent of the rats have placental scars (which resulted from implantion of the placenta). The Baltimore residential rats attain the 50 per cent point at a smaller size (compare ratios) than do the warehouse rats. The farm rats did not attain a 50 per cent point. Since the pres-

ence of placental scars is interpreted to mean that the female has had young, these data show that the Baltimore residential rats produce young at a relatively small size compared with other populations.

Data for Roof Rats (Table 5B) are available from Thomasville (Georgia), San Antonio (Texas), Tampa (Florida), London, and Cyprus. Again the 50 per cent points are very similar for the various places. Harrison (1951, p. 682) calculated the weight at which 50 per cent of male Roof Rats have abundant sperm. The weights varied from place to place for three races of Roof Rats between 57 and 75 grams. For the small *R. exulans* the value was 22 grams.

TABLE 5B

Size of Roof Rats at Sexual Maturity

PLACE	HABITAT	50% POINT		RATIO		REFERENCE
		g.	mm.	g.	mm.	
Scrotal Testes						
Tampa, Fla.	urban	56	115	.45	.79	Davis, unpub.
Georgia	rural	—	132	—	.82	Ecke, unpub.
Berlin	urban	—	146	—	—	Becker (1952)
Perforated Vaginal Orifice						
Tampa, Fla.	urban	56	128	.53	.95	Davis, unpub.
Georgia	rural	—	126	—	.76	Ecke, unpub.
Berlin	urban	—	153	—	—	Becker (1952)
Ovulation						
London	urban	93*	—	—	—	Watson (1950)
Cyprus	urban	88	—	—	—	Watson (1950)
Placental Scars						
Thomasville, Ga.	urban and rural	97	158	.88	.97	Davis, unpub.
San Antonio	urban	—	163	—	.95	Davis and Emlen, (1948)
Tampa	urban	109	161	1.04	1.19	Davis, unpub.

* Approximate.

The data in this section show that the force of reproduction is acting at all times in rat populations, since there is no period of the year without production of young. In many cases there is a maximum twice a year but in other cases only once a year. Considerable variability from year to year means that almost every study of a population will have to collect data to determine the breeding for that year, and that data for other years can rarely be extended to a particular year. Tables 3A and 3B show that the number of embryos per year per female is roughly the same for the two species. Norway Rats have a few large litters; Roof Rats have several small litters.

Mortality

In contrast to the force of reproduction, the force of mortality causes a decrease in the population. For present purposes a knowledge of the actual causes of death are not needed, because the death rate is the pertinent aspect of problem. In this paper death rate is defined as the number of deaths per rat per year, which is the number of deaths during a year divided by the average population. The probability of dying is defined as the number of deaths in a group divided by the initial number in the group (Davis, 1952a). The following methods for studying death rates have been used with varying success. (1) In large populations it is sometimes possible to find enough dead rats of known age to determine the death rate. (2) It is possible to calculate the probability of dying of marked rats in a population, thus obtaining a

figure for the mortality of rats after marking. (3) It is theoretically possible to determine the death rate of adults in a stationary and closed population by a knowledge of the proportion of adults in the population, since an adult must die for each young animal that reaches maturity. In practice, this method encounters difficulties. (4) It is possible to calculate the death rate if the birth rate and the population are known (Davis, 1951a).

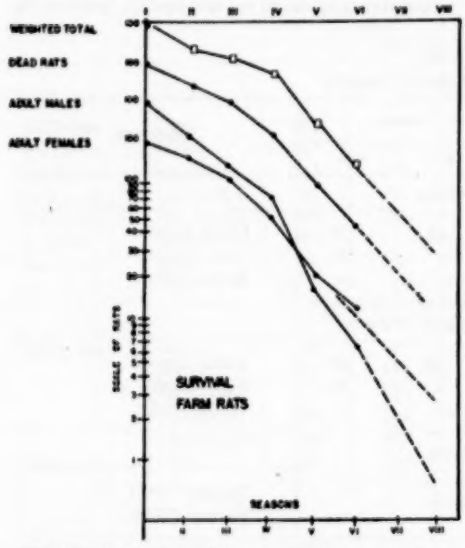


FIG. 13. SURVIVAL OF NORWAY RATS ON A FARM, IN PERCENTAGES OF ORIGINAL NUMBER

The scale is arithlog, and the base line is shifted for each curve to prevent excessive overlapping. The weighted total represents the survival of all rats irrespective of age or sex. The dead rat curve represents the actual mortality of 60 rats that were found dead. The curves for adult males and adult females show the higher rate for males. (See text and reference for details.)

The first two methods were used by Davis (1948b) to determine the death rate on a farm near Baltimore, Md. (Fig. 13). From this figure it is apparent that only about 5 per cent of a given number of rats are alive at the end of 12 months, and that the females live longer than do the males. This study has a number of deficiencies. Since no satisfactory criteria of chronological age exist, the rates are not age-specific except for the crude distinction between adults and young. Furthermore, the "trappable" population declined from 1100 to 600 during this time, and hence the death rate may be atypical, although, of course, reproduction may have been deficient. Similar data for rats marked, released, and recaptured in the city of Baltimore were entirely unsatisfactory because the rats learned to avoid the traps. A study of mortality rate on a declining population in Hawaii (Spencer and Davis, 1950) gave a very high probability of death (50 per cent in 42 days). Harrison (1951) presents a few data for Roof Rats in Malaya and gives a probability of dying of 0.3 for 4 months, or 0.97 for a year.

A calculation of the annual death rate can be made from data for rats captured in residential blocks of Baltimore that were known to have stationary populations. It is arbitrarily assumed for this purpose that a rat weighing less than 100 grams was born during the month when captured. Since the population is stationary, a rat must have died for each rat born, and hence the total deaths of rats weighing more than 100 g. within a month is equal to the number of rats weighing less than 100 g. For these calculations the probability of dying plus the probability of survival equal one. Of 1036 rats captured in blocks with stationary populations, 176 (17%) weighed less than 100 g. Hence the monthly probability of dying is 0.17, and the monthly probability of survival is 0.83, for rats weighing more than 100 g. The annual probability of survival can be obtained by raising the monthly rate to the twelfth power, to give 0.087. The annual probability of dying is therefore 0.913, or about 91 per cent. The probability of survival may be used to determine the death rate from the equation $p = e^{-d}$ where p is probability of survival and d is death rate. The annual death rate thus is 2.44 rats per rat for rats weighing more than 100 g.

A calculation may also be made from data for the birth rates, since the populations are stationary. Table 3A (Baltimore, 1947–49, stationary) gives a mean of 10.3 embryos per pregnant female and an incidence of lactation of 4.3. If we assume that the number of young is reduced to 8.3 by weaning time and that the incidence of weaning (not lactation) is 4.0, then these females weaned about 33 young per year. Therefore 33 rats must die during the year for each pair of adult rats. This gives an annual death rate of 33/2 or 16.5 per breeding rat per year. This value is much higher than the above values because it is age-specific for weanlings. The values obtained above are for trapped rats and thus neglect the high juvenile mortality from weaning to a "trappable age."

A study of the mortality of young during the pregnancy and lactation of the parents (Davis, unpub.) is possible from an analysis of reproductive data. A Baltimore population (Table 3A, warehouses for 1946) averaged 9.4 embryos and had an incidence of pregnancy of 4.8. This means that $9.4 \times 4.8 = 45$ embryos are present at the 16th day of pregnancy. The incidence of lactation was 3.5, and if we assume that there is an average loss of 2 young rats, and 0.5 litters, then there are $7.4 \times 3.0 = 22$ sucklings at the midpoint of lactation. Therefore, the probability of surviving from the 16th day of pregnancy to the midpoint of lactation is $22/49 = .49$ for 25 days. This value may be translated into annual terms by suitable calculations, to give an annual probability of dying of 0.999 for this phase of the life of a rat.

The calculations in the above paragraphs are frankly crude attempts to get an approximation of the order of magnitude of death rates of wild rats. The necessity of resorting to such calculations is evidence of considerable ignorance rather than a statement of knowledge.

The probability of dying or egress of alien rats introduced into a strange environment is very high (Calhoun, 1948), being around 0.84 per month in contrast to 0.51 for native rats.

The available data indicate that the females live longer than the males. The study of disappearance rates (Davis, 1948b) showed that females lived about 20 per cent longer than males. A comparison of length of life may be made from changes in the sex ratio also. The data of Schein (1950, p. 493) and Leslie, Venables, and Venables (1952) show a low proportion of males among large Norway Rats, a ratio which may be interpreted as indicating that the males die off faster than the females. Harrison (1951, p. 677) found an increase in the proportion of females with size for *Rattus rattus diardii* in Malaya. But for several less common forms the proportion of males increased. An increase of males was found for Roof Rats in Cyprus (Watson 1951, p. 12) and Georgia (Ecke, unpub.). Because of differential growth rates of males and females, data of this type are difficult to interpret.

Movements

The difference between immigration into and emigration from a unit area is the migration rate and may be a force for increase or decrease according to its net value. In general, vertebrates tend to live within a small area for a period of time until death or a radical change of environment occurs. The size of an individual's home range varies according to the species and the condition of the area. It was no surprise, then, to find that Norway Rats have a limited home range (Davis, Emlen, and Stokes, 1948). Three methods were used to study the extent of movement: (1) mark, release, and recapture individuals and analyze distances between captures; (2) feed methylene blue to rats and determine distribution of dyed feces; (3) follow tracks of individual rats in fresh snow. From these studies it was found that rats live for many months within an area of 100 to 150 feet both in residential areas of Baltimore and on a farm. Table 6 includes data published by Davis, Emlen, and Stokes (1948) and also additional unpublished data for city rats obtained by Calhoun and Davis. Additional data for farm rats, obtained by Davis during 1949–51, agreed with the data given in Table 6.

Watson (1951, p. 33) found limited movements of Roof Rats in Cyprus. Of 166 recaptures of males, 67 per cent were within 50 yards; of 115 recaptures of females 77 per cent were within 50 yards. Some recaptures were as much as 200 yards from previous capture. McDougall (1944–6) found limited movement in *Rattus concolor* in Australia.

In Germany Kemper (1950) studied rat tracks in snow and found limited movements. His map (p. 236) shows a range of about 45 meters between food and harborage for a colony, but in another area the range was greater. Clearly the extent of movement depends upon the distribution of food, harborage, and barriers.

Having established the fact that rats have a limited home range, the rate of immigration or emigration remains to be considered. No studies exist that concern this rate specifically, but an idea of its magnitude can be obtained from various lines of evidence. On the Baltimore farm, in 73 cases rats were recaptured in a different building, while in 757 cases rats were recaptured within the same building. Thus only about $73/830 = 0.089$ or 8.9 per cent of the rats moved among 4 buildings, which were only 20 to 100 feet apart. This means that during the 183 trapping days of the study $.089/183 = .00048 = .048$ per cent of the population went to another building per day. Since the population on the farm that year averaged about 820 rats, the daily movement rate from one buidiing to another is about $0.00048 \times 820 = .4$ rats.

In the city only 1 of 312 recaptured rats went from one block to another. It was further estimated (Davis, Emlen, and Stokes 1948, p. 220)

that only 10 per cent of the rats crossed the alleys. Additional evidence from the study of the populations in blocks indicates a low order of magnitude of movements. For example, one block remained free of rats for 2.5 years even though rats were present in adjacent blocks. The populations in blocks with low rat populations that were adjacent to blocks with high populations increased no faster than did populations in blocks that were adjacent to blocks with low populations. The available evidence thus indicates that the rate of movement from block to block is very low and may be considered negligible. The rate of movement from colony to colony within a block is probably higher.

TABLE 6

Home Range Results

(distance between successive captures)

CITY RATS

DISTANCE IN FEET	MALES		FEMALES		TOTAL RATS	PER CENT
	Rats	Per cent	Rats	Per cent		
0–19	65	44	85	48	150	46
20–39	47	32	50	28	97	30
40–59	20	13	23	13	43	13
60–79	8	6	9	5	17	5
80–99	3	2	5	3	8	3
100–199	3	2	4	2	7	2
200 plus	3	2	0	0	3	1
Total	149		176		325	

FARM RATS

	ADULT MALE	PER CENT	YOUNG MALE	PER CENT	ADULT FEMALE	PER CENT	YOUNG FEMALES	PER CENT	TOTAL RATS	PER CENT
Same building										
0–19	66	36	67	45	76	36	107	51	316	42
20–39	89	49	74	49	122	57	86	41	373	49
48–59	23	13	8	5	13	6	13	6	57	8
60 plus	4	2	1	1	3	1	3	2	11	1
Total	182		150		214		209		757	
Different building	24		17		22		10	73		

Thus far, the discussion of movements has assumed a relatively constant environment. Obviously, if the habitat changes radically the rats will be forced to search for new homes. Errington (1935) found that extensive movements of Norway Rats occurred in the fields between summer and winter. Chapman (1938) reported an exodus of rats from a flooded corn field and Llanos (1944) recorded extensive movements after the sugar cane harvest in Argentina. Aisenstadt (1945) reported movement in the spring from the houses to the forest and a return in the fall. Mass migrations are frequently reported (Rust, 1946; Lantz, 1909), but their causes are seldom apparent. The extension of range (Silver, 1927; Tryon, 1947) that has occurred throughout the world is probably principally due to human agencies rather than the rat's own legs. Although in many ports only a negligible number of rats come off the ships, Przyborowski (1948) reported a great increase in the proportion of Norway Rats in Poland caused apparently by the fact that Roof Rats were not brought in during the war because of a reduction of shipping.

The converse of changing the rat's environment is to put the rat into a different environment. Long ago in New Orleans, Creel (1915) liberated 294 rats that had been obtained in various parts of the city and recaptured some as far as 4 miles from the

point of liberation. This experiment is the basis of the widespread notion that rats are extensive wanderers, but it merely shows that rats liberated in a strange environment may travel long distances. Even under these circumstances only 22 per cent were captured more than 1 mile from point of liberation. Calhoun (1948) studied the movements of alien rats released in a city block in Baltimore. Although only 1 alien rat was found outside the block, only 16 per cent of the aliens were recorded within 2 months after release. The reason for the few recaptures is probably high mortality, but in any case alien rats did not remain in a strange environment.

To summarize this section on the forces that affect rat populations, it may be said that the reproductive rate is fairly well known and is about 20 to 30 young weaned per adult female per year. The probability of dying is poorly known, but is approximately 0.90–0.95 per year. The movement rate is fairly well known to be very low in constant environments but to be very high in changing environments. However, the high death or egress rate of alien rats means that few rats become established in new areas if these already have rat populations.

POPULATION FACTORS

Various factors of the rat's environment influence and control the population forces. These can be grouped for convenience into three interacting categories: (1) habitat, (2) predation, and (3) competition. The discussion of these three groups of factors will mention their effect on the population forces.

Habitat

The structural, climatic, and nutritional factors are called the habitat. Within limits they are density-independent, i.e., their effect is not proportional to the number of rats in the population. Practically nothing is known about the effect of climate (temperature, humidity, etc.) on the rat population beyond gross observations that rats are absent from the arctic regions except in a few cities. The seasonal changes in reproductive rate presumably are due to changes in weather, but no analysis is available. The death rate and also the rate of movement may be influenced by weather conditions, but again data are lacking.

Little is known about the nutritional requirements of wild rats. Stokes found (Emlen, Stokes, and Winsor, 1948) that rats in Baltimore ate an average of about 25 g. of ground corn per day, and Chitty and Shorten (1946) obtained an average value of about 30 g. of wheat. The vast literature on white rats does not clarify the problem because the contents of the rat's food (garbage) in urban areas are not known in detail.

Schein and Orgain (1953) studied the preference, consumption, and weight changes in rats that were fed various single items in domestic garbage. They found that the change in weight was proportional to the logarithm of the calories in the food ($r = +0.76$). Also the change in weight of a rat was found to be proportional to the logarithm of the preference of a rat for a food when given a choice between it and a standard diet ($r = +0.72$). Naturally the logarithm of the calories is proportional to the logarithm of the preference, but there is much scatter ($r = +0.56$). The relation between the caloric value of a food and consumption of it suggests that a rat strives to eat a constant number of calories (about 56 cal. per 100 g. of rat per day) if the types of food are suitable. These studies are preliminary but mark the beginning of an understanding of the food requirements of wild rats.

A serious but necessarily still preliminary attempt to measure the environmental conditions has been made in urban blocks in Baltimore (Orgain and Schein, 1952). The complexities of the conditions, as well as our lack of knowledge of the physiology of the needs of the rats, make the results very tentative. However, the importance and uniqueness of the data justify their inclusion in this review. The method consists of crudely measuring the quantities of food, fences, junk, etc., available to rats in each yard in a residential block. The units are simply 1, 2, 3. From a correlation of these units with the presence or absence of rats in each yard a value was obtained that puts our arbitrary units into a scale that has some meaning as to rats. (See original paper for details).

These units may be plotted to show the changes that occur in a block during a period of time (Figs. 14, 15). In these cases changes in rat population are fairly well correlated with changes in the environment. Data in Table 7 show the changes in environmental units in 2 blocks that were rehabilitated and in one reference block. The decrease in rat population in the 2 rehabilitated blocks is correlated with environmental changes in the block, while no great change occurred in the reference block.

The units may also be used to determine what

specific factor limits a population at a particular time. From a consideration of Liebig's law of the minimum it appears that some factor that is correlated with the rat population should be the limiting factor, whereas uncorrelated factors are present in excess of the rat's requirements. Thus in Fig. 15 for August, broken paving, an aspect of shelter requirements, was probably the limiting factor and its increase would permit the increase of the rat population till some other factor became limiting. Conversely, the reduction of some other factor might make it the limiting factor, so that now the quantity of broken paving would be excess. This, in fact, occurred between August and January

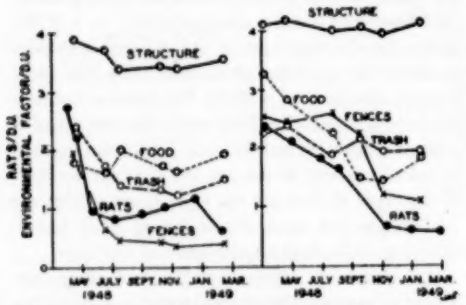


FIG. 14. CHANGES IN ENVIRONMENTAL FACTORS IN TWO RESIDENTIAL BLOCKS

The rat population (heavy line) and the fences, trash, food, and structure in environmental units per dwelling unit are shown. Note that the decline in rats was correlated with a decline in number of fences and trash but without any significant change in food or structure. In the second block the decline in rats was correlated with a decline in food and afterwards in number of fences.

when the food supply appeared to become the limiting factor.

This experimental approach to the problem of environmental factors was pursued till it became obvious that the crudity of measurements and the practical difficulty of changing the environment by a known amount prevented any degree of precision. Furthermore, it became obvious that the rats were very adaptable and could utilize a great variety of objects for shelter. Attention was therefore directed at food in an attempt to determine how much was needed per rat per day.

As has been shown by others (Chitty and Shorten, 1946) the total food consumed by a colony of wild rats will increase to a plateau level. However, Orgain and Schein (1953) found that the consumption returned to this plateau within a couple of days of the removal of 30 to 50 per cent of the estimated number of rats that were feeding there. This result is interpreted to mean that a large number of rats were kept away by competition with other rats.

These studies represent a start on the analysis of the environment. They present some crude methods of measuring the factors in terms of the rat's needs and also a theory to guide the measurements. The results are naturally meager at this stage.

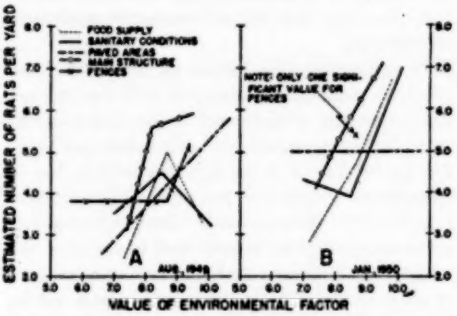


FIG. 15. CHANGES FROM AUG. 1949 TO JAN. 1950 IN CORRELATION OF RAT POPULATION TO THE ENVIRONMENTAL FACTORS

Note that the "paved areas" in August were proportional to the abundance of rats but in January were not. Main structure showed little change. The food changed from not proportional to proportional.

Predation

This aspect differs from the physical environment because theoretically it varies in its effect with the density of the population. For example, the number of rats eaten by cats should depend not only upon the cats but also upon the number of rats. When rats are abundant the cats should eat a high proportion of the population, but when rats are scarce the cats should eat a low proportion. It should be noted that these statements are only theory, since data are not available for the predatory relations of rat populations.

Predation obviously does not affect the reproductive rate except through its action on mortality. The extent of the effect of predators on mortality is poorly known. There is no evidence that in Baltimore cats affect population sufficiently for the effect to be detected by the census method. Jackson (1951) found that an average cat ate about 25 to 30 rats a year in residential areas of Baltimore. However, there was no evidence that this predation

altered the size of the population, since the arrival or disappearance of a cat in a block did not measurably affect the number of rats present. Apparently the cats merely killed rats that were doomed to die from other causes. At any rate, the effect of cats cannot be detected by the crude measurements (involving a 10 per cent error) of population.

In Baltimore, there is no correlation between the number of dogs and of rats in city blocks (unpub.). In spite of the pride of cat and dog owners, the only substantial effect on the population seems to be a possible limitation on the invasion and establishment of rats in new areas. Peters (1948) found in Germany a positive correlation between the presence of rats and of cats. Apparently, the conditions that bred cats also bred rats. In Baltimore, the food for dogs frequently encourages the rats. Indeed, the largest rat every caught (720 g.) was trapped under the kennel of a well-fed dog. For other regions there are generalized statements that mongooses controlled the rats in some West Indian Islands (Schwartz, 1942) or some of the Hawaiian Islands (Doty, 1945, p. 83).

Predation may also be studied by removing a certain number of rats each month. From the rate of increase of the rat population in a block, the increase in the number of rats per month may be calculated. When this number of rats is removed each month, the block should remain at a constant population. The appropriate number of rats was removed from each of 4 blocks for from 7 to 15 months and from 6 other blocks for shorter periods. The calculations indicated that the monthly removal of a very small number of rats (around 4 per cent of the population) should keep the block at a constant population. But instead, when this calculated number was removed the population fluctuated up and down irregularly. It is concluded that the changes in the environment were far more forceful than this predation and were a more important factor in population changes.

Pathogens are of course predators of a type and also require consideration. Rats from several places were examined (Davis, 1951c) for the presence of three microorganisms. The spirochaete *Leptospira icterohaemorrhagiae* was found to have a high prevalence (around 50 per cent in all places), to have no relation to population changes, and to have no relation to rat weight. The nematode *Capillaria hepatica* had a similar relationship to its host. It was concluded that these two organisms are well-adjusted and have little effect on the host.

However, the bacterium *Salmonella* spp. was found in only 4 per cent of 974 rats but in high prevalence in 2 blocks. Furthermore, a sharp epidemic occurred on a farm in 1946 and produced some mortality. The population recovered from these outbreaks and it was concluded that salmonella has only a temporary effect on the number in a population.

The use of pathogenic organisms to control rats

TABLE 7

Environmental Measurements

DATE	STRUCTURE	ARBITRARY JUNK	UNITS FOR PAVEMENT	FOOD	FENCES	NUMBER OF RATS
Rehabilitated Blocks						
April 16, 1948	8.2	9.0	8.6	8.2	8.8	152
July 14, 1948	7.8	8.1	7.3	8.2	6.5	58
Change	−0.4	−0.8	−1.3	0.0	−2.3	−96
April 15, 1948	9.0	9.4	10.0	8.9	10.4	92
January 20, 1949	7.6	8.1	7.3	7.7	7.2	22
Change	−1.4	−1.3	−2.7	−1.2	−3.2	−70
Reference Block						
June 9, 1948	9.0	8.9	9.0	8.8	8.8	94
February 23, 1949	9.1	9.4	10.1	9.2	8.6	108
Change	+0.1	+0.5	+1.1	+0.4	−0.2	+12

has been tried for half a century, with generally unsatisfactory results (Rosenau, 1910). A recent test (Habs and Heinz, 1951) was confused by the subsequent use of red squill poison (ratinin), but no epidemic was initiated. The pathogen used has generally been some strain of *Salmonella* (Leslie, 1942).

A test of the effects of a pathogen on a population of rats was made by introducing *Salmonella enteritidis* into a population known to be free of infection (Davis and Jensen, 1952). The rat population in February, 1950, was considered to be free of salmonella because more than 300 rats, examined over the previous 2 years, were all negative. The tests for salmonella were determination of agglutinin levels of sera obtained by heart puncture and culture of cloacal swabs and of feces. (It is recognized that this must be regarded as only an "index" of infection). The rats lived on a farm in 4 buildings and were trapped alive in box traps, marked by clipping toes, bled and swabbed, and released at the place of capture. During the two years of the study about 2000 individual rats were caught, and there were about 3000 recaptures.

It was clearly demonstrated that the bleeding from the heart had no effect on the mortality except for an occasional accident.

In February 1950, 20 rats in one building were inoculated with a culture of salmonella. Then in October 1950 another group in the same building and a group in another building were inoculated.

The effect of the pathogen can be determined by making a comparison of the recaptures of infected and non-infected rats. Since the tests used did not always detect the infection, the terms "positive" (infection demonstrated) and "negative" (infection not demonstrated) are used. The data reported describe the period from October 22, 1950 till October 23, 1951, and divide the rats into male and female for comparison. The data are complex to analyze, but probably the simplest valid comparisons are among the various groups at the 16th week. Of 111 positive rats, 30.7 per cent were recaptured and of 218 negative rats 39.0 per cent were recaptured. The difference is not significant ($P = 0.134$). Indications that this method of analysis would show up a difference between types of rats, whenever a difference exists, is available in a comparison of the recaptures of males and females, which should show a greater number of recaptures for females than for males. Of 162 males, 29.6 per cent were recaptured; of 167 females, 42.5 per cent were recaptured. This difference is significant ($P = 0.007$). The inference of greater survival of female rats accords with other data.

Another aspect of the study was the spread of the infection on the farm. The infection after the first inoculation was limited to two buildings. After the second inoculation the infection was limited for the winter to the two buildings the rats of which had received salmonella, but in spring, at a time of change in the barns, the infection quickly spread to the other two buildings.

The effect of salmonella on reproduction could either be a decrease in reproduction due to direct pathogenicity or a compensatory increase due to a decrease in population. An analysis of reproduction during the endemic of salmonella can be made by comparing lactation figures. The proportion of mature females from whose nipples milk can be expressed can be used to compare the number of suckling litters at various times or places. The true number of litters is of course not known, but its value is unnecessary to detect changes if we assume that the same ratio between the true number of females lactating and the index (expression of milk) holds at various times or places. The evidence follows: Before inoculation in February 1950, one area had an index of 10.1 (104 rats) and another area had an index of 11.5 (75 rats). From February to October, 1950, the lactation index for 508 mature females was 13.5 in the first area (which received salmonella) and for 319 mature females was 17.3 in the other part (without salmonella). After inoculation of both areas in October 1950 the index was 18.1 (494 rats) in the first and 5.3 (373 rats) in the second. Both areas had similar indices of infection. Although differences in lactation occurred, they are not demonstrably related to the presence of the pathogen. This experiment demonstrates that a pathogen may have a negligible effect on mortality and reproduction under certain conditions and also that the spread may vary greatly according to local changes.

One interesting aspect of predation is mentioned by Matheson (1943). In theory, at least, a predator-prey system should be cyclic. As the number of rats increases, the number of persons killing rats should increase and thereby cause a decrease in the number of rats, which would be followed by a decrease in the number of persons killing rats, and so forth. In England the number of rats killed has fluctuated even though the number of rat-trappers was constant. Therefore, Matheson concludes,

these changes were not attributable to a predator-prey cycle.

Predators may have some effect in causing rats to move from one yard to another and also in preventing the invasion of a yard uninhabited by rats. These effects have not been studied quantitatively however.

Competition

This factor, like predation, is dependent upon population size for its magnitude. The term competition is used, as indicated by Solomon (1949, p. 15) to mean the direct struggle between individuals for a limited supply of environmental necessities.

This dependence derives from the fact (Calhoun, 1949) that the rats in a colony are organized in a social hierarchy. Some individuals are dominant over others in the terms of fighting and other behavior. The social rank of an individual is of basic importance in the forces of reproduction, mortality, and movements.

Calhoun (1949) found that the reproductive rate of females that lived near food was greater than that of females that lived far away. For example, 10 litters were weaned out of 12 pregnancies among females near the food, while only 1 litter was weaned out of 12 pregnancies in females living far away. Apparently the strife to get to food affected the survival of the young.

Davis (1951d) found that the annual incidence of pregnancy was significantly higher in increasing populations (6.1) than in stationary populations (3.8). Since the increasing populations were below capacity for the area, it seems likely that the reduced competition permitted more frequent pregnancies. However, the annual incidence of lactation was the same in both types, thereby indicating a greater loss of litters in the increasing populations. The same relationships occurred on a farm.

Asdell (1941), using laboratory rats, studied the relation of age to reproductive rate. He found that rats that bred early or late in their reproductive life were less prolific than rats that bred normally. These data suggest that, if rats breed late because of competition at times of high population, the total number of young would be reduced.

Davis (1951b) also concluded that, after a population of rats had been reduced to 50 per cent of capacity, the remaining rats rapidly gained weight. This agrees with the results of Calhoun (1950), who found that dominant rats gained weight more rapidly and were heavier than subordinate rats. Also there was a loss in weight of the entire colony at a time of social tension.

Competition obviously will tend to increase the death rate. Calhoun (1952) found an increase in the number of body wounds with age and noted that high-ranking individuals had fewer wounds than low-ranking ones. The wounds rarely cause death directly but frequently permit infection and debilitation.

In several cases (Davis, 1949c) the rat population in blocks has declined when rats were introduced. These results were interpreted to indicate that the newcomers had set up a social turmoil that interfered with normal reproduction. The possibility that an introduction of disease caused the decline is difficult to rule out, but studies of the pathogens do not provide evidence for the latter explanation.

Competition clearly may affect the force of movement, although quantitative data are hard to obtain on this point. Calhoun (1952) found that subordinate rats were driven out to the edges of the area. Also Calhoun (1948) found that the introduction of rats in a block did not cause the native rats to move. However, the introduced rats rapidly disappeared, at least in part due to movements from the block. It seems plausible that in high populations severe competiton forces subordinate rats to move in search of more favorable places. However, the mortality must be great and apparently few survive. The high-ranking members of colonies matured more rapidly than did the low-ranking rats. Furthermore, there is a suggestion of differences in the prevalence of some pathogens. Slowly maturing rats appeared to have a higher probability of dying than the other rats.

These results suggest the conclusion that competition is frequently the mechanism that sets the stage for death, either directly or indirectly.

The problem of territorialism (the defense of an area) has recently been studied. Steiniger (1950a) found that rats did not eat or remove baits that were marked by rat urine or feces. He also (1950b) described the possession of a territory within a colony, and stated that the defense of a territory begins after pair formation. A consequence of territorialism, if it occurs in rats, is that some individuals are driven away. Such competitive mechanisms as hierarchy and territorialism serve to keep the population within the limits set by the environmental resources.

DISCUSSION

The preceding sections have summarized our present knowledge of the characteristics of rat populations. Each of the three primary population forces is of course the resultant of the population factors at a given time. One group of factors (habitat) in its action is independent of the size of the population (N). Another group (competition) is probably proportional to some power or other function of N (Davis, 1952b). Let us consider the effect of these factors on the tendency of the population to maintain equilibrium. The first factor (habitat) obviously influences the location of the equilibrium (or asymptote). Any change in physical environment is followed by an adjustment of N to the new value. The two factors, predation and competition, however, are functions of N and thus adjust to the situation. For example, the result of increased competition is to reduce the reproductive force and increase the mortality force. Both these effects tend to reduce N and hence reduce competition. Thus a displacement in one direction is soon automatically cancelled.

It is not the purpose of this paper to discuss the theories of limitation of population, since there are several recent reviews of that subject (Solomon, 1949: Hutchinson, 1948; Crombie, 1947). However, a description of the changes in the number of rats in Baltimore since 1943 may be worth-while to illustrate certain characteristics of rat populations. The population declined from about 400,000 in 1944 to 165,000 in 1947 and to 65,000 in 1949 (Davis and Fales, 1950). The force of reproduction probably was about the same over this period, since in 1943 the number of embryos per year per adult female was $9.9 \times 4.7 = 46.5$ (see Table 3) and in 1947–1949 it was $10.1 \times 4.9 = 49.5$ embryos. It can be concluded that there was at least no decline in embryos during the decline in population. The force of mortality was not studied in the 1943–45 period and hence cannot be compared. The force of movements was probably similar in both periods.

There are few data about the population factors in Baltimore. However, an extensive program of housing rehabilitation has greatly reduced the available harborage and food. It is clear that the reduction in population resulted from lowering the ability of the city to support rats. It seems likely that predation increased locally when a protective habitat was destroyed. Also, competition must have increased because of the reduced supply of food and harborage. Presumably these two factors were the mechanism for increasing the mortality to bring the population into equilibrium with a lowered habitat capacity. It is probable that the quality of the food supply that was available to a live rat was the same in the two periods, because the mean lengths of more than a thousand rats measured in each category did not change. The data are: 1943–45, male—202.9 mm.; female—204.4 mm.; 1947–49, male—202.9 mm.; female—200.3 mm. Obviously no change in length has occurred. These data seem fragmentary when viewed in perspective and should emphasize the magnitude of the task of obtaining adequate quantitative data to describe the forces controlling a population.

A postscript on the control of a population is pertinent. Our modern knowledge suggests a general principle (Davis, 1949c) which was, some time ago, mentioned by Barrett-Hamilton (1910), Donaldson (1925), and Eaton and Stirrett (1928) briefly in respect to food supply. To manage a population the habitat should be altered in such a direction as to change the asymptote. Factors such as predation and competiton, which are proportional to N, need not be altered since compensations will occur. These factors are really controlling factors in the sense that they keep the population at the asymptote. For the practical use of persons who desire to increase or decrease a pest, it is clear that managing the habitat is the proper procedure. Fortunately the proper direction of alteration is given by density-dependent factors (predation and competition). The general principle is to alter the environment so that the density-dependent factors will change inversely to the desired change in population. Specifically for rats, this means that in order to decrease the number of rats, the food and harborage supply should be decreased so as to increase the competition among the rats.

This review has brought together a mass of data from a variety of sources and attempted to organize the results so as to facilitate understanding of natural populations as a whole. It cannot be claimed that striking new truths have been clearly revealed, but some points merit mention. The changes in populations are often predictable from a sigmoid curve, but variation in conditions causes each population to have its own particular curve. Reproduction as a population force varies much less from place to place and time to time than does

mortality (although data for mortality are meager), and hence emphasis on mortality studies is justified as a means to understanding population changes. The habitat is fundamental in the determination of population size, but the density-dependent factors (predation and competition) are the means of holding the population within the limits imposed by the habitat. For rats, competition as manifested by social organization is the more frequent mechanism for limiting the population and thus deserves increased attention.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

THOUGHTS ON CHROMOSOME BREAKAGE

BY C. P. SWANSON

Johns Hopkins University

A review of SYMPOSIUM ON CHROMOSOME BREAKAGE, *Held at the John Innes Horticultural Institution, 9–11 June, 1952. Supplement to Heredity. Vol. 6.*

Oliver & Boyd, London and Edinburgh. $7.50 (paper). viii + 315 pp. + 11 pl.; text ill. 1953.

Since the late 1930's, when Sax began his radiation studies on *Tradescantia* chromosomes and the Cold Spring Harbor group initiated similar investigations on *Drosophila* sperm chromosomes, emphasis in radiation cytogenetics has been preeminently quantitative. This approach was both understandable and necessary, since the relationships between frequencies of aberrations and the physical data would form the background for any physiological work. Emphasis was therefore given to a study of the types and the time of appearance of various aberrations, and the relationship of these types to dosage, intensity, dose-fractionation, and the cell cycle. This period of research, which extended through the war years, may well be termed the descriptive phase of radiation cytogenetics, although it was becoming increasingly clear that the frequency of aberrations, as the end result of any given dose of radiation, was capable of modification by factors other than the radiation itself. A considerable refinement of the descriptive aspects of the problem was made by Lea and Catcheside in England, but it was soon obvious that future progress in any understanding of radiation effects would come through a physiological approach. As Darlington has pointed out, "Chromosome studies have long promised to become a kind of visible chemistry. This promise is now being realized."

The physiological trend was of course foreshadowed by studies of the effects of temperature, oxygen, and mixed radiation, as well as by the rapid development of chemical mutagenesis. The early disregard of the fact that the rate of cell division was disturbed by radiation, and of the scoring of breaks and reunions separately brought on a severe criticism and a reassessment of radiation data by Darlington and his group. That this reassessment has been and will continue to be profitable one can little doubt, for although it was early recognized that the production of an aberration involved two distinct events—breakage followed by healing, and reunion or restitution—it can be fairly stated the circumstances surrounding the initial induction of a break and the subsequent history of the broken ends are but little understood. The existence of potential breaks, whatever their nature might be, further complicates the problem. That these aspects are central to an understanding of the physiology of radiation effects is self-evident, and it is therefore encouraging to witness the attack being made on them by the English workers.

There has been to date remarkably little need for a revision of the ideas which emerged from the earlier radiation studies, and it has been only recently that some of the basic concepts have been questioned by the Darlingtonian school of thought. The criticism has been sufficiently vigorous to split the field of radiation cytology into two distinct schools, that of Darlington and his coworkers on the one hand, and that of Sax and Catcheside, the late D. E. Lea, and their students on the other. The split stems in a certain sense from differences in aim, but there is also a fundamental disagreement as to the interpretation of experimental results, a disagreement accentuated by the fact that it is virtually impossible for one not intimately connected with this area of research to distinguish between fact and conjecture in the published writings of Darlington. Darlington, to be sure, has long been a distinguished and stimulating contributor to the discipline of cytogenetics, but even the casual reader can readily detect that in his writings the arm of inference is long indeed and at times very tenuous, and that reiteration often

plays a dominant role in transposing speculative thought into seemingly proven fact without the benefit of critical experimentation. The cryptic jargon employed has further contributed to the confusion.

This symposium is, then, in part at least, a reflection of the point of view of Darlington and his followers on the subject of chromosome breakage. Its importance, however, is not to be measured by the disagreements existing between the two schools of thought: i.e., disagreements as to the nature of isochromatid aberrations, as to the breakability or unbreakability of prophase chromosomes and heterochromatin by x-rays, or as to the interpretation of the results of fractionated doses, to mention the more obvious ones. Rather, the importance of the symposium is to be measured by the fact that it attempts to delineate, face squarely, and do something about the problem regarding what happens, or can happen, between the introduction of a mutagenic influence—radiation or chemical—into a cell and the appearance of a changed character in the cell or in the organism. This is approached by dividing the symposium into four sections, interrelated to be sure but separable at least for convenience: Radiation Breakage, Chemical Breakage, Secondary and Spontaneous Breakage, and General. Much of the material is presented here for the first time, making an over-all appraisal at this time not only premature but also unjust.

The first section is largely the work of Darlington and his students, and since the several papers adopt rather exactly the terminology and interpretations of breakage introduced by Darlington and La Cour in the 1945 volume of the *Journal of Genetics*, the errors are similar and consequently are compounded. The errors revolve about the interpretation of the origin of the isochromatid type of aberration; and although the value of separating breakage from reunion is clearly a step forward, Thoday, in a later chapter, shows quite conclusively that the earlier interpretation of Sax is correct, and that Darlington's insistence that the sister chromatids of a split chromosome in prophase cannot be broken by a single path of ionization, and that isochromatid aberrations arise by breakage in an unsplit resting chromosome followed by reunion of sister chromatids after the prophase split, is not to be taken seriously. Indeed, if further proof is needed that isochromatid breakage is a real phenomenon, this is provided by the demonstration of Kirby-Smith and Daniels (*Genetics*, 38: 375–388. 1945) that there is a pronounced 2-hit component in the dosage curve which causes a significant departure from the linearity demanded by Darlington's hypothesis. That this departure is the more pronounced the shorter the wave length is in complete agreement with the target theory criticized by Darlington. The qualitative and temporal distinction between chromatid and chromosome breakage is therefore a valid one, and to merge the two categories, as Koller occasionally does in his study of the effects of low intensities of radiation, serves only to obscure rather than to clarify the events taking place.

The chapters by Lane and Haque continue to emphasize a discrepancy in experimental results obtained from fractionation of the dose in *Tradescantia*. Why their data are quantitatively different from those of Sax and Giles is difficult to imagine, but the answer seems not to be in experimental technique, since de Serres and Giles' recent study was carried out according to the method used by Lane, but without confirming his conclusions. Certainly Lane's severe criticism of Sax's temperature controls is without foundation. The studies of Darlington, La Cour, and Haque on the effects of radiation on meiotic cells point out the possibilities of this approach to the analysis of breakage and reunion, (as Sparrow has done). Once again, however, the long arm of inference weaving in and out among the fragments of data will leave the reader grasping for a single solid fact upon which he can focus attention.

The second section, on Chemical Breakage, brings out quite forcibly the fact that chemical and x-ray breakage are not to be qualitatively equated. The studies of Oehlkers, Revell, and McLeish all indicate a selectivity of breakage in heterochromatin as contrasted with euchromatin, while Fahmy and Bird confirm the earlier results of Auerbach that mutations chemically induced are associated with far fewer gross aberrations than are those induced by ionizing radiations.

Part Three confines itself to a consideration of secondary and spontaneous breakage, the former term covering those deferred breaks not directly related to the initial effect of radiation. Evidence bearing on the effect of an extra-nucleolar organizer (a heterochromatic effect?) in reducing x-ray breakability is presented by La Cour, while the interesting behavior of dicentric chromosomes in somatic cells is considered by Koller, Darlington and Wylie, and Hair. Rees' discussion of a centromeric control of chromosome splitting and breakage is not quite convincing. Auerbach concludes this section with her studies of chemical mutagenesis which show that various stages of gametic development in *Drosophila* exhibit a differential pattern of sensitivity, and possibly suggest a variety of ways by which mutations can be induced.

The last, and more general, section is concerned with the synthesis of desoxyribose nucleic acid (DNA) in normal and irradiated cells and its relationship to breakage (Walker, and Howard and Pelc), a theoretical discussion of chromosome behavior in terms of a polymeric system of molecular orientation (Ambrose and Gopal-Avengar), certain chemical effects on chromosomes (Loveless), a presentation of the target theory and recent developments which necessitate a broadened point of view as well as a reconsideration of the nature of isochromatid aberrations (Thoday), and lastly a brief comparison of breakage by different agents (Gray).

Apart from the papers by Oehlkers, Auerbach, Howard and Pelc, Thoday, Gray, and a few others, which can be readily appraised and understood, the symposium presents the philosophy, techniques, and approaches of the Darlingtonian school of radiation cytology. As such it cannot but stimulate those working in the field. Indeed, if the past provides any clue to the future, the points raised here will send many a cytologist scurrying to his radiation laboratory to confirm or to deny. On this score, the symposium can be said to have achieved a measure of success. As a comprehensive and penetrating synthesis on the subject of chromosome breakage it can only be considered incomplete and decidedly biased.

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GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

MATTER, MIND AND MEANING.
By Whately Carington; Preface by H. H. Price. Yale University Press, New Haven. $3.75. xxii + 257 pp. 1949.

This is a most amazing book, by a widely read gentleman who during his lifetime was one of the foremost authorities and pioneers in the field of psychical research. The work, which was unfinished at the time of his death, is a philosophical "anti-philosophy" treatise intended, in the words of the author, "to clean up once and for all ... this muddle about the relation of Mind to Matter, which has fretted philosophers ever since philosophizing began." Carington also had two other axes to grind. One, to relieve himself of some of his hostility towards philosophy, particularly metaphysics—he is overfond of quoting such passages as Bertrand Russell's remark, "Philosophy, from the earliest times, has made greater claims, and achieved fewer results, than any other branch of learning." The second unstated raison d'être is to revise our fundamental concepts so that certain "queer facts" related to "supernormality" or "paranormality"—i.e., certain events which do not seem to make sense—will not seem queer, but will be accepted as reasonable and to be expected. In other words, if one can be led to the "proper" understanding of meaning, mind and matter, and their interrelationships, only a few easy steps (down the primrose path?) remain in order to "introduce some sort of intelligible order into the whole field of 'supernormal' happenings."

The stages of Carington's attack begin with the statement that the only entities whose existence we can be certain of are "sensations," "sensa," or as he prefers to call them, "cognita." Matter, he says, consists of nothing else. With these cognita are associated others which follow on one another "in a manner conforming to that of past experience," so that we are assured that we see a material object. If it does not fit with our past experience the object is not real but a hallucination. "That is to say, any material object is a ... sequential pattern of cognita ...." Any reference to properties of things, or substances as such is, according to Mr. Carington "mythological foolishness." Physiologists, biochemists, and physicists are, consequently, mythologists. On this basis, perhaps one can think of Einstein as a Theseus leading us through the labyrinthine complexities of time and space—and with the assistance of other Herculean scientific associates cleaning out some of our intellectual Augean stables, leaving one corner, however, for Mr. Carington to call home (be it ever so humble!).

To follow the Caringtonian thesis a bit further, a mental object (?) is defined as a cognitum sequence "of the type specified by the laws of psychology." These sequences are of the "spirit" as well as of the "mind." Mind *is* a series of cognita and it would then follow, that consciousness cannot be a property of the mind. We have now reached the pièce de résistance: "A cognitum is not only a part of the entity cognized, it is also a part of the cognizing mind. The difficulty of how Mind can act on Matter or vice versa, therefore disappears, Matter and Mind are not qualitatively different 'orders of reality,' or the like, but inseparably interlocking and interwoven organizations or patterns of the neutral and irreducible entities or particulars (cognizable) of which the universe is composed." Oh what a tangled web we weave! We can now have no difficulty accepting hallucinatory, psychic, or psychokinetic phenomena.

Although Carington, like some other philosophers, feels both dualism (Cartesian) and interaction (brain-mind) to be untenable, for many physiologists these

concepts are the most acceptable on which to base investigations of the problems of brain and mind. Sherrington, Adrian, and others have certainly made this clear. That mind can act on matter is a postulate that the scientist can discuss on somewhat better grounds than Carington's. It has been suggested, for example, that the behavior of matter could be controlled by mind within limits set by the Heisenberg Principle of Uncertainty. In a recent discussion of these problems, Eccles points out that this hypothesis "could form the physical basis of the neurophysiological hypothesis that has been developed for mind-brain liaison." Some of the neurophysiological postulates suggest that mind produces changes in the matter-energy system of the brain and so must be in that system itself. This would lead us to a two-way mind and matter pattern similar to the one Carington suggests. The major thing, however, is that we have arrived at this point in what appears to be a much more reasonable way, and realize that such a deduction is based on present physical hypotheses—hypotheses which may change and which cannot take certain factors into account. Perhaps future data will help to explain spatio-temporal patterning in the nervous system and ultimately clear up Carington's attempt to settle the mind and matter problem.

R. G. GRENELL



PRACTICAL ESSAYS ON MEDICAL EDUCATION AND THE MEDICAL PROFESSION IN THE UNITED STATES. *By Daniel Drake; introduction by David A. Tucker, Jr. The Johns Hopkins Press, Baltimore.* $2.50. xvi + 104 pp. 1952.

It is enlightening indeed to find that some of the problems which most concern the top medical educators of today were recognized and discussed very poignantly at least 120 years ago. In reading this reproduction of seven essays originally published in 1832, one is impressed not only by the professional stature and modest spirit of Daniel Drake, but also by the sincere reverence in which he held his profession. Although he was a product of the apprentice system of medical education, and wrote at a time when the standards for former medical education were very low, Drake was an ardent proponent of the university and hospital mode of medical training, and constantly urged the improvement in both quantity and quality of formal instruction for physicians.

Among the causes for error in the medical and physical sciences, Drake lists: (1) the disproportion between the strength and grasp of our intellectual faculties, and the number and variety of objects upon which they are to be exercised; (2) the attempt to arrive at philosophical truth without due preparation; (3) errors in early education; (4) fickleness of attention; (5) forming conclusions while we should still be observing; (6) vividness of fancy; (7) impatience; (8) pride; (9) excessive deference for authority; (10) a defective love of truth; and (11) a defective ambition. A more damning list of human frailties would be hard to imagine.

In writing about those who are afflicted with vividness of fancy, Drake provides the following gem: "They suppose themselves men of genius, when, in fact, they are endowed with but one of its attributes. They are great builders of hypothesis, but all their pyramids are inverted. They never investigate closely, but to sustain a pre-conceived notion, and then instinctively reject every fact which militates against it. Their ardor and obstinacy are often so great, as to inspire confidence in their opinions, and make proselytes of those who should labor to expel their delusion and bring them back to the sober realities of the external world. Such an enterprize, would, however, in most cases, prove ineffectual; and hence students and young physicians, should guard vigilantly against the earliest illusions of this *ignis fatuus* of the mind."

Drake would undoubtedly be dismayed to find that the same human defects which weighed so heavily upon him in 1832 are still with us in 1953, and still impede the progress of science.

B. AUBREY SCHNEIDER



BIOLOGY: HISTORY AND BIOGRAPHY

THE ALCHEMISTS—*Founders of Modern Chemistry. By F. Sherwood Taylor. Henry Schuman, New York.* $4.00. x + 246 pp. + 12 pl.; text ill. 1949.

This is a fascinating book. Its purpose, which is magnificently fulfilled, is to give a short and clear account of the alchemists, their ways of thought, and their contribution to man's achievement. This was not an easy task, inasmuch as the available material is not complete, much of the work has not been carefully studied, and, what is even more difficult, such an account necessitates an understanding of thought habits quite different from ours. A description of this nature could have become overly long, desiccated, and uninteresting. Quite to the contrary, Sherwood Taylor has written a most "readable" but still scholarly and well-documented book which should have wide appeal among all readers of science, history, and detective stories.

To many people the alchemist is either a mystical, slightly offbalance character of a long bygone medieval era, or a humorous concept symbolized either by the Sorcerer or his Apprentice. Taylor shows these views to be entirely invalid, even though he is quite clear concerning the erroneous basis of the central ideas of alchemy. He is able to resolve some of the contradiction involved and to pick out the gifts of the alchemists

which have formed the foundations of modern chemistry.

The history is traced from the earliest signs and symbols through its development in different parts of the world (there is a most interesting and unusual discussion of alchemy in China, for example) to its relationships to science as a whole, and more particularly to chemistry. It is made clear that alchemy was not merely a "get rich quick" device, but was a creed the ramifications of which spread into many aspects of human thought and behavior. It was essentially religious. "Its philosophy aimed at the unification of all nature in a single scheme, the author of which was avowed to be God." It is most interesting that from this faith and devotion should come to us one of the alchemist's major contributions—the origin of chemical laboratory techniques which enable us to overcome blind faith by questioning, examining, and experimentation.

Everyone will be intrigued by this story. It is well written and beautifully printed and illustrated. There is appended a bibliography for those who wish to delve further into the original sources.

R. G. GRENELL



ECOLOGY AND NATURAL HISTORY

UNTERSUCHUNGEN ÜBER DIE ZUSAMMENHÄNGE ZWISCHEN EXPOSITION, RELIEF, MIKROKLIMA UND VEGETATION IN DER FALLÄTSCHE BEI ZÜRICH. *Pflanzengeographische Kommission der Schweizerischen Naturforschenden Gesellschaft. Beiträge zur geobotanischen Landesaufnahme der Schweiz, Heft 29.*

By Jerzy Fabijanowski. Hans Huber, Bern. S. fr. 13.50 (paper). 104 pp. + 5 pl. 1950.

Bulletin Number 29 in the series of contributions to the Swiss geobotanical survey is an investigation of the relationships between exposure, relief, microclimate, and vegetation in the Fallätsche near Zürich. The author compiled the material for this paper while working as an assistant at the Silvicultural Institute of the Eidgenössische Technische Hochschule in Zürich, Switzerland.

The Introduction emphasizes the fundamental role of the plant-sociological status and the successional stadia in an area considered for forestation. Great significance is also attributed to the relationship between relief and exposure, on the one hand, and microclimate and vegetational development, on the other. The author holds that even the synecological differences within relatively small areas should be considered in forestation under the extreme conditions found in the mountains. Although there is a large literature available on microclimatic questions, the relationships fundamental to forestation techniques are little known.

An area for study had to be chosen on which the various phases of vegetational development from the pioneer plant communities to the forest could be observed, and also where variation in the terrain permitted examination of a multitude of microenvironments. At the same time, it was important that natural conditions should have been influenced by human activity as little as possible.

The Fallätsche, a semicircular erosion slope at the headwaters of the Rutschli Brook near Zürich, was chosen because it most nearly met these requirements. The Fallätsche is on the eastern slope of the Albis Mountains at an elevation of about 600 to 780 meters above sea level. The area includes about eight hektares, five of which are forested. Information about the overall climate, geologic formation, soils, and the general vegetation pattern is given in the introductory part of the paper.

The second part contains a description and discussion of the studies conducted by the author in the Fallätsche. These studies include a vegetation survey, as well as measurements of temperature, humidity, and evaporation. A section called "additional studies and observations" deals with the germination and development of seeds and seedlings under both laboratory and range conditions. Measurements of biological activity in the oils are included.

The survey of the vegetation was made in order to "describe the plant communities of the Fallätsche, especially the successions which lead from the pioneer communities to the climax communities; that is, to the durable communities. At the same time an attempt was made to clarify the relationship between the developmental stages of the vegetation and the individual factors of the habitat (exposure, relief, slope, and local hydrologic conditions). Both together should make it possible to describe the site, which is the basis for decision in forestation and other silvicultural considerations." Computing the results of the survey in tabular form, the author presents a picture of the general trends of plant succession in the Fallätsche. It is stated that the development of the vegetation parallels the stabilization and maturation of the soils. All stages from the pioneer vegetation to fragments of forest were found on the steep slopes.

Quantitative measurements of biological activity in the soil were made by a method devised by F. Richard. Cellulose test cords were dug into the ground and left there for a certain length of time (46 days in this study), after which they were taken out and subjected to a tearing test. The tearing modulus of the cord was then used as a measure of the biological activity in the soil. According to Richard, this method indicates "the total of bio-physical and bio-chemical processes in the soil which can be attributed to the activity of higher plants, microflora, microfauna, as well as higher animals." Greater biological activity was found in places that had a vegetation cover than in bare areas.

Since the observations were made on a limited area, the author warns the reader against making generalizations. He believes, however, that the study corroborates the opinion that even synecological differences on relatively small areas are significant in the forestation of mountainous country. It is important for the practicing forester to be able to recognize microenvironments without complicated special measurements. The differentiation of planting areas on the basis of existing groundcover is therefore desirable. The author assumes that recognizable successional stages give the safest criteria for the recognition of forestation units.

JOHN J. STRANSKY



DIE WIRTSCHAFTLICHE UND KULTURELLE BEDEUTUNG DER BINNENGEWASSER, *mit besonderer Berücksichtigung Deutschland und angrenzender Gebiete. Die Binnengewässer, Vol. XVII.*

By Hermann Helfer. F. Schweizerbart'sche Verlagsbuchhandlung (Erwin Nägele), Stuttgart. DM. 50.00 (cloth); DM. 47.00 (paper). xiv + 286 pp. + 40 pl. and 2 folded maps. 1949.

This treatise on the economic and cultural significance of inland waters resembles some recent books on U. S. water resources in scope, but without the political sermons. There are many pretty photographs of streams, canals, and lakes in Germany, and there is a chapter devoted to literature about fresh water (especially poetry). While the book includes a summary of limnological investigations and a review of the fisheries of fresh water (in which the conflict with power interests is discussed), it seems to be primarily intended for the use of economists and geographers rather than limnologists.

JOEL W. HEDGPETH



HIGH JUNGLES AND LOW.

By Archie Carr. With illustrations by Lee Adams. University of Florida Press, Gainesville. $4.50. xviii + 226 pp.; ill. 1953.

Four and a half years in Honduras, teaching at Escuela Agrícola Panamericana, and countless forays into the jungles and cloud forests of adjacent Central America gave Archie Carr such an emotional attachment for the land and its people that his account alternately glows and races along like a first-class adventure story. The Honorable Rafael Heliodoro Valle, Ambassador from Honduras to the United States, contributed an enthusiastic testimonial as a foreword to the book; and well he might. For *High Jungles and Low* makes one long to sit quietly in those same jungles with senses reaching out into the unpredictable. "The brief sunset spread flame through the clouds behind the western ranges, and desultory shreds of mist began to spiral down into the milpa. For once there was almost no wind, and the only sounds were occasional incredibly sweet passages from the *jilgueros* and the low, duotone chant of the Mexican trogon in the depths of the forest. . . . Then three quetzals, a female and two gorgeous males, rose above the crown of the tree. One of the males and the female flew directly into the woods, but the other flew and hopped from one tree to another, dashing out of the tree and back, making vertical sallies into the air above and descending again in a wholly uncalled-for series of swoops and dips and pirouettes to display his crimson breast, the blue-green fire of his wings, and the grace of his yard-long tail. This was reward enough, and indeed if the forest grew for no other end than to support this bird it were no waste."

The book is divided into four parts: The Land—from the cloud-forests to the lowland jungles and the eroding land where the inhabitants have difficulty raising adequate crops in the depleted soil; People in the Land—with a series of stories told as incidents that give a glimpse into the troubles and quiet joys of the native population; The Sweet Sea—concerning the relict salt-water fishes in fresh-water Lake Nicaragua and the history of this region; and Halls of the Mountain Cow—telling of a trip into the jungles on a timber survey and the various animals (including the tapir, the "mountain cow") met with and eaten.

There is a good index, but even those who have experienced the jungle are likely to use it more than in most books. Carr uses the local Spanish names more extensively than the English ones for the animals and plants and sometimes one must look to the second or third reference before finding the more familiar equivalent. The *jilgueros* mentioned in the quotation above are identified as nightingale thrushes at the second but not at the first or last of the three times it is mentioned. Nightingale thrush is not indexed, nor thrush, nightingale. Those who have become familiar with the agouti in Panama as *ñequi* must add *guatuso* to their vocabulary if they are to keep up with the Honduran account without looking in the back of the book. And the collared peccary becomes *sajino*, not *zajino*, which keeps the phonetics nearly identical but is two pages off in the index!

Those who love the tropics will revel in Carr's account. Those who plan to go there should read the book the better to understand what they will experience. And all who have to do with the improvement of hemispheric relations should make a point of digesting well the whole of the chapter called The Wasting Land, in which the supreme need for help in conservation is shown as the key to aiding both nutrition and public health, and the field in which least has been attempted. More people with sympathetic understanding will have to follow Carr before much progress can be made in helping the people to help themselves.

LORUS J. & MARGERY J. MILNE

AQUARIUMS. *Dover-Foyle Handbooks.*

By Anthony Evans. Dover Publications, New York. 60 cents (paper); $1.50 (cloth). 115 pp. + 12 pl.; text ill. 1952.

This member of the Dover-Foyle Handbook series stresses "how-to-do-it." Equipment needed for keeping fish indoors and out, and a discussion of "troubles" from diseases, parasites, predators, and unsuitable water form the serious beginning and end of the little volume. The central 22 pages on cold-water fish, goldfish, and tropical fish, and 7 more on fish breeding are more suitable bait for those wishing to join in this absorbing hobby.

LORUS J. & MARGERY J. MILNE



FRESHWATER AND SALT-WATER AQUARIA.

By Francis G. W. Knowles, with eleven plates in half-tone and seventy illustrations in line by the author. George G. Harrap & Company, London, Toronto, Wellington, and Sydney; [British Book Center, New York]. $2.75. 174 pp. + 11 pl. 1953.

"It is hoped that this book will serve as a guide-book for the beginner and a reference work for the accomplished aquarist, to help them to enlarge their experience and to avoid catastrophe." For the beginner, Knowles provides diagrams and a discussion of means for aerating all manner of receptacles. For the expert there is an extremely brief section on the effect of pH variations. Chapters on Facts About Fish and on the common animals and plants of both fresh and salt water place considerable emphasis on what may be brough indoors for observation rather than on types to be bought from the supply house.

LORUS J. & MARGERY J. MILNE



BETWEEN THE TIDES.

By Philip Street, illustrated with photographs by the author. Philosophical Library, New York. $4.75. 175 pp. + 32 pl.; text ill. 1953.

While this book adds little that is new to the interminable stream of sea and shore-books, it is written in a pleasant, informal manner which should stimulate rather than discourage the "young naturalist" on British shores for whom it is intended. It is unfortunate that the illustrations did not receive as much attention as the text; the drawings are amateurish (why do compilers of such books continue to think that sloppy drawings are acceptable for children?) and most of the photographs are of obviously dead animals laid on glistening rock or mud, so that it is often hard to distinguish the subject from its background.

JOEL W. HEDGPETH

THE COMMON LOON IN MINNESOTA. *Minnesota Mus. of nat. Hist., Univ. of Minnesota. Occasional Papers: No. 5. Paper No. 2679 of the Scientific Journal Series, Minnesota. Agricultural Experiment Station.*

By Sigurd T. Olson and William H. Marshall. The University of Minnesota Press, Minneapolis. 75 cents (paper). vi + 77 pp.; ill. 1952.

Facets in the life history of loons have been woven together to form this interesting resume of two summers of careful observation. Among some of these observations may be mentioned that loon chicks have two downy plumages; that territorialism is exhibited by pairs, and the territories are established immediately upon arrival on the breeding grounds—52 such territories were located in the study area. Of 54 nests, 52 were on small islands, 2 eggs being the normal clutch, and the 29-day incubation period is shared by both parents. In 1950, 35 of 57 nests failed, principally because of predation or desertion. Twelve of 27 pairs which lost eggs renested once, three pairs renested twice. Productivity of the loon population was low. Out of the theoretical possible production of 84 young, only 21 young were reared successfully. In the 60-sq.-mile nesting area, the population during the nesting season was estimated to be between 109–114 adults (42 nesting pairs, 10 non-nesting pairs, 5–10 singles), rising to 128–143 birds during the brood season. The authors are to be congratulated on a fine piece of field work which must have entailed considerable physical effort. There are many illustrations, bibliographic references to other observations on loons, and tables and maps. At first it was sometimes difficult to differentiate the original work of the writers from that derived from the literature, but as the study progressed into the population aspects it became quite clear that important original material was at hand.

HENRI C. SEIBERT



EVOLUTION

SCIENCE SPEAKS. *An Evaluation of Certain Christian Evidences.*

By Peter W. Stoner. Van Kampen Press, Wheaton. $1.50. 91 pp. + 4 pl.; ill. 1952.

Each of us in his own way and according to surrounding experiences, environment, and tradition, builds a base upon which a code of living rests. This base may be broad or narrow, may have as its core a religious faith, or may involve only an areligious code of ethics. To the Fundamentalist, however, and such is Professor Stoner, the Bible provides the poured concrete which both firmly fastens this base to solid ground at the same time that it provides an outward form to the structure. The various splinter factions among the Fundamental-

ists attest to the fact that the outward form differs as interpretations of the Bible differ. Professor Stoner, however, is not concerned with this outward aspect; rather he is seeking to reinforce his poured concrete with the steel rods of scientific fact. He seeks to do this by providing a scientific basis for the 13 claims made in Genesis. It probably will not be out of place to recall to scientists that in Genesis, Chapter I, God is claimed to have created heaven and earth, and all its inhabitants therein; but what is more important to Professor Stoner, God is also claimed to have created things in a definite order. Thus creation of heaven and earth was followed in order by light and darkness, firmament and water, plants, sun, moon and stars, fish, fowl, earthly creeping things, and finally man in his own image. There are of course minor discrepancies such as the sun coming after the plants, and whales being included among the fishes, but in general these can be reinterpreted so that on the face of things the order of creation is much as we would have expected on the basis of what we now know of astronomy, geology, and evolution. Genesis, on the other hand, was written long before we knew of these things, and it is Professor Stoner's contention that the only recently discovered facts of astronomy and geology now permit us to see that some of the early disputes about the authenticity of Genesis, as the Word of God, resulted from imperfect scientific knowledge. Genesis and scientific fact, however, are now in complete rapport, and Professor Stoner has marshalled his evidence with the result that he has calculated on the basis of probability that anyone seeking to predict the correct order of creation without a previous knowledge of existing facts would have about one chance in 311 million of collecting a bet. Ergo, the writer of Genesis was guided by the hand of God. In fact, the author states, "If it were written by man, representing the scientific ideas of the time, we should expect to find all of its definite statements in error." His opinion of his fellow man is low.

Those who have seen the light will find the present arguments superfluous; indeed, the intelligent Protestant will find that the author has fallen into the commonest error of using only these facts which bolster his hypothesis, and of discarding or controverting those which do not. For example, his discussion of the theory of evolution is not only misleading; it displays an abysmal ignorance of recent evolutionary studies. One can only presume that his treatment of astronomical and geological facts is similarly biased, and those who might feel the need for reassurance in such matters are likely to find the author's rods of steel to be nothing but crumbling pencils of clay. As for the reviewer, the saying that "The Sabbath was made for man, not man for the Sabbath" still holds.

C. P. SWANSON

GENETICS AND CYTOLOGY

THE GENETICS OF THE MOUSE. *Second Edition, Revised and Enlarged.*

By Hans Grüneberg. Martinus Nijhoff, The Hague. Guilders 45.00. xiv + 650 pp. + 17 pl.; text ill. 1952.

This excellent book is a thorough revision of the first edition, enlarged to include 8 more years of work, represented by 600 new references, in this field. As was to be expected from the first edition, it is scholarly, critical, stimulating, and clearly written. Since Grüneberg's books are already well known and enthusiastically appreciated by mammalian geneticists, it will be the purpose of this review to emphasize what is mentioned in the Preface, but is not apparent in the title, namely, that this book is intended for all biologists who work with mice and as an aid in medical research. Fifteen chapters, more than two-thirds of the text, deal with inherited anomalies in the various organ systems: integument, endocrines, nervous system, blood, skeleton, etc. However, genetics takes up only a minor part of this space, most of which is devoted to a description of what is known of the anatomy, physiology, and embryology of the defects. It is here, and in the chapters on Reproduction and Growth, Quantitative Differences, Resistance to Infectious Diseases, and Genetics of Cancer, that there is a wealth of material of interest to medical research workers and experimental biologists who use mammalian material. Workers in these fields who have used Grüneberg's *Animal Genetics and Medicine* will find *The Genetics of the Mouse* valuable as an up-to-date supplement for more detailed information. Of special interest to geneticists are chapters on chromosomes and linkage, induced genetic changes, and gene action. The 1751 references are classified under 64 subject headings.

W. L. RUSSELL



GENERAL AND SYSTEMATIC BOTANY

TEXTBOOK OF BOTANY. *Revised Edition.*

By E. N. Transeau, H. C. Sampson, and L. H. Tiffany. Harper and Brothers, New York. $6.00. xi + 817 pp. + 1 pl.; text ill. 1953.

This textbook is quite different from most of those intended for beginning courses in general botany, and the authors make a great deal of the fact that nearly every chapter has been written to be read *following* the making of observations and the drawing of inferences by students, or after class discussion. However, it is conceivable that it might be read as a guide to making such observations and inferences. The authors lean over backwards "to avoid language patterns charac-

teristic of abandoned ideas and interpretations" (personified and anthropomorphic interpretations). One is led to suspect that many students (and maybe some instructors) will find themselves confused rather than edified, at times. The drawing of "best inferences" (scientific conclusions, principles, natural laws, etc.) after specific observations and references is a worthy aim and one with which we might all agree although success might depend on whether the materials for such inferences are adequate, whether the student is intellectually able, and whether the instructor is capable and "on his toes."

As to the content of the book, it seems better in the coverage of physiological than of morphological material, it is excellent for its emphasis on the interrelationships of parts of the plant and the ecological relationships of plant organisms, but the material which might serve for a survey of the plant kingdom is somewhat meager, and those who look for an evolutionary thread will find it tangled or undiscernable. Common, everyday things about plants and their economic and human welfare aspects are given in abundance, are well integrated, and should appeal to the "general-education-minded." Certain chapters, such as those on the Seasonal Aspect of Plants, Vegatative Multiplication, the Origin of Plants Used by Man, and the Vegetation of North America will prove interesting and informative reading for any student or amateur botanist.

It seems to me that this revised edition has little to recommend it over the original text, but that those who liked the original will doubtless approve this revision, while those who preferred other textbooks will not choose this one even though it has been revised. Certainly the present "edition" should be considered merely a revision, as the title page indicates, and not as a second edition, even though in the Preface the authors speak of "the major changes in the second edition." I was unable to find much that was new or any very striking improvements to justify calling it a second edition. However, as the authors indicate, there have been corrections of errors and some simplification of discussions, as well as a much revised and more adequate index, more references at the ends of chapters, and certainly some of the material has been brought up to date. We find alleles, antibiotics, apomixis, aureomycin, and bacteriophage included in text and index, to mention a few subjects, but it is disappointing to find no reference made to the rejection of the principles of Mendelian inheritance in Soviet Russia.

A misleading reference found under "acknowledgments," is that to "many new drawings." To imply that there is much new illustrative material does not seem justified, since of the 424 figures in both original and revised texts, there have been only about 30 changes, some of which are doubtful improvements, some merely slight enlargements or better prints, and others very slightly modified diagrams.

CARROLLE ANDERSON MARKLE



TEXTBOOK OF PRACTICAL BOTANY.

By R. C. McLean and W. R. Ivimey-Cook. Longmans, Green & Company, London, New York, and Toronto. $7.50. xxiv + 476 pp.; ill. 1952.

The first part of a projected four-volume work, *Textbook of Theoretical Botany*, appeared in 1951 (*Q.R.B.*, 28: 176. 1953), and dealt essentially with a survey of the plant kingdom, together with brief sections on cytology, histology, and evolutionary morphology. The other volumes are presumably in preparation, but in the meantime the authors have felt the need of a companion laboratory volume which could be used in combination with their already published textbook as well as for the remaining 3 volumes to come. The present book is the answer to this need. It is a compact and thorough volume, and like the earlier textbook, it is designed to meet the laboratory requirements for all aspects of botanical study excepting that more commonly found at the graduate level. Its design and contents obviously are scaled to an English botanical curriculum that is far more continuous in time and subject-matter than is usually encountered in American colleges and universities, so that despite the high merits of the book as a laboratory guide and manual, it is unlikely to find favor among teachers who have come to look upon botany as a series of one-semester courses. Laboratory teachers, however, should find many valuable suggestions which they could themselves utilize to advantage in either general botany, physiology, or ecology.

C. P. SWANSON



THE ALGAE OF ILLINOIS.

By Lewis Hanford Tiffany and Max Edwin Britton. The University of Chicago Press, Chicago. $10.00. xiv + 407 pp.; ill. 1952.

The present volume is the second part of a floristic treatise on the algae of Illinois. It is essentially the provision of keys, descriptions, and diagnostic illustrations in a plan to provide a manual for general use. The first part of the treatise, *A Catalogue of Illinois Algae* by M. E. Britton, was published by Northwestern University in 1944, and gave distributional records of the species, county by county, as well as a bibliography for the algae of Illinois. The present volume does not repeat that information. However, such records as have been established since the appearance of the earlier volume, e.g., the interesting report of *Wislouchiella planctonica* found in pools in Coles County

by K. E. Damann, have been added. It has been the intent of the authors to complete their distributional information by the inclusion of such data and by the addition of records published since, or inadvertently omitted from, the first volume. The 5-page bibliography includes only citations of this additional literature and the literature peculiarly pertinent to the new volume. A concise 6-page glossary is included along with an index.

Almost all the species are illustrated by uniformly redrawn figures from various sources. One could have hoped for original drawings from the skilled pen of Jane Roller, the illustrator, whenever specimens were available. The authors felt that this was impractical in cases where good previous illustrations were available. The figures are assembled on full-page plates in such a way that they appear as near as practicable to the textual material. For this the authors are to be commended, as the use of these figures is thus considerably facilitated.

The introduction is valuable. It is essentially a resume of the algal habitats of Illinois and their history, with a presentation of the authors' opinions on phylogeny and their circumscriptions of the phyla. It is not surprising, but nevertheless gratifying, to note that here two more leading phycologists are accepting the major groups of algae as discrete phyla. The authors prefer to consider all seven phyla, such as the Rhodophyta, Pyrrophyta, etc., as members of a plant kingdom. The phylum Chlorophyta, while not including the Charophyceae, is restricted to algal forms.

The present-day diatoms are included, as are other groups which are optically inconspicuous but of prospective ecological importance, such as the euglenoids and blue-green algae (I often think "blue-green bacteria" would be a better term for the latter). One suspects, from the roster of species, that in Illinois attention might well be given to the soil algae and such unicellular forms as those among the Chrysophyta, which have proved to be of such indicator or synecological importance whenever studied closely. The former would well merit a considerably detailed study extending far beyond their taxonomy or floristics, though even this elementary step has not yet been taken anywhere in North America in detail. Study of the unicellular forms indicated is particularly pertinent in Illinois, where stream and pond pollution are common problems.

The University of Chicago is to be commended for producing this technical volume in such pleasing typography and format at a minimum cost to the consumer. The authors' well conceived and executed design of the descriptive and illustrative material has provided the most complete general algal flora yet attempted for any single state. Thus this book can be expected to be the basic reference volume for the algal flora of Illinois for many years to come. As such, it is a very desirable item for both biologists and libraries.

M. Doty

THE FUNGI. *A Description of their Morphological Features and Evolutionary Development.*

By Ernst Albert Gäumann; translated and arranged by Frederick Lyle Wynd. Hafner Publishing Company, New York and London. $10.00. 420 pp.; ill. 1952.

To American mycologists familiar with Gäumann's *Die Pilze: Grundzüge ihrer Entwicklungsgeschichte und Morphologie*, published in Switzerland in 1949, it comes as no surprise that an English edition has appeared. This is at least the third book by Professor Gäumann to be translated into English. Unlike the earlier *Comparative Morphology of Fungi* by Gäumann and Dodge, the translator has in this instance adhered fairly closely to the original German text.

The classification adopted is on the whole conservative and somewhat simplified. Myxomycetes are not included, and the Fungi Imperfecti are dealt with in only the briefest fashion. Perhaps the greatest break with traditional schemes of classification is to be noted in the case of the Archimycetes, considered by Gäumann to represent a class, coordinate with Phycomycetes, Ascomycetes, and Basidiomycetes, and composed of organisms considered by others as belonging to groups as diverse as the Myxomycetes, Chytridiales, and Lagenidiales. Gäumann rightly concludes that a thorough understanding of the relationships of these forms is not possible on the basis of current knowledge.

The illustrations are numerous and well done. Many of them are original, having been prepared for the earlier German edition by Heinz Kern and Ernst Lehmann.

In addition to a presentation of the principal features of the morphology and taxonomy of fungi, the author has given an account of the phylogeny and evolutionary tendencies of the fungi, employing this unifying theme throughout the book.

Frederick T. Wolf



MANUAL OF THE NORTH AMERICAN SMUT FUNGI.

By George William Fischer. The Ronald Press Company, New York. $8.75. xii + 343 pp.; ill. 1953.

"This manual is a taxonomic treatment of the smut fungi (Ustilaginales) of the North American continent. ....In general, annotations concerning biological features such as spore germination, life history, control, etc. have purposely been omitted." The bibliographical references are few, being confined to those of importance in the identification of the smuts. Other references are given in full in the author's recent work, *The Smut Fungi*.

In this manual there are recognized 22 genera, 276 species, and a few varieties, on species of 242 host genera. The author distinguishes the species chiefly on

the basis of the morphology of the fungi. Species distinctions based solely on the host are mostly not recognized except on the host-family basis. Thus there has been a considerable combining of species that in some publications have been kept distinct. As an example, we find the loose smuts of barley, rye, and wheat united as one species with the name *Ustilago nuda*, because the morphological differences of the fungus on these hosts are insufficient to warrant distinction on the species level. The author gives over 20 synonyms, based on different hosts, for *Ustilago striiformis*, and over 8 species epithets for synonyms of what he combines as *Cintractia caricis*. It is apparent that the number of recognized North American species of smuts would be far greater than given above if *host* species had been the main character for species distinction.

The description of almost every recognized species was made by the author from studies of the type material, where available, or of authentic specimens of the species. The illustrations represent all but about a half dozen of the accepted species. In most of these the spores are shown, and in many the infected host.

In addition to combinations of species, some genera have been united. Thus *Doassansiopsis* (in part) and *Setchelia* are united with *Doassansia* under the latter name. On the other hand, *Tuburcinia* and *Urocystis* are kept distinct, contrary to Liro and some other mycologists.

The manual begins with a "host genus index and key to the species of North American smut fungi." The host genera are arranged alphabetically and not in accordance with their family relationships. Thus the smut *Ustilago violacea* appears in 5 widely separated places in the keys and *Entyloma compositarum* in 22 places. Between 110 and 120 species of smuts are accredited to the grasses, about 30 to the sedges, 10 to composites, and about 8 to the Ranunculaceae. No distinction is made in this key to keep the Tilletiaceae and Ustilaginaceae apart. Following this key are the descriptions of the genera and their included species. The genera are arranged alphabetically, without family assignment, and the species within each genus are also in alphabetical order. No attempt is made to group near each other those species found on related hosts. A result of this alphabetical arrangement is that the adjacent genera may represent very dissimilar fungi and the adjacent species often are very unlike. Only 1 species is described here as new to science; *Ustilago sonorians* Zundel sp. nov., though a good many species names are changed by transfer or combination. The genus *Graphiola*, sometimes, but often with doubt, ascribed to this order is not included.

ERNST A. BESSEY



CACTI AND SUCCULENT.

By G. Gilbert Green. The Pitman Publishing Corporation, London, New York, and Toronto. $7.00. 238 pp. + 91 pl.; text ill. No date.

As with so many of the English garden books reaching this country, this one is characterized by an over-all excellence of treatment: it is eminently readable, the coverage is thorough, the illustrations are clean and useful, and the index is workable. Similarly, the price is a bit stiff. Classification and description of the cacti follow the phylogenetic treatment and the nomenclature of Britton and Rose. This makes for a great wealth of names to confound the amateur, and it would seem that the simpler nomenclature, as used by Lyman Benson in his *Cacti of Arizona*, would have been more appropriate and in line with current taxonomic practices. The succulents other than cacti are treated alphabetically by genera, and include a rich selection of world-wide species. Cultural procedures are outlined in some detail, yet they are sufficiently understandable for even the neophyte to proceed under a full head of steam and with reasonable hope of success and satisfaction. Although written presumably with the British gardener in mind, the volume is in no way regional in usefulness, and the gardener, be he amateur or professional, restricted or diversified, will find this a worthy investment.

C. P. SWANSON



TREES AND TRAILS.

By Clarence J. Hylander. The MacMillan Company, New York. $3.00. x + 237 pp.; ill. 1953.

This book will doubtless have popular appeal to the amateur naturalist and hiker who is satisfied with a condensed and somewhat generalized description of various forest regions in the United States. It is in no sense a taxonomic or silvical manual; but the average reader will learn unavoidably to recognize the important tree genera of this country, as well as gain considerable knowledge about their ecology and uses. The book seems especially designed for those nature lovers who, by profession or necessity, are prevented from spending all of their free time in the country, and are thus compelled to experience vicariously much of their pleasure in nature. The book is abundantly and effectively illustrated by halftones and line drawings.

SCOTT S. PAULEY



FLORA OF THE CHARLESTON MOUNTAINS, CLARK COUNTY, NEVADA. *Univ. Calif. Publ. Bot., Vol. 24. By Ira W. Clokey. University of California Press, Berkeley and Los Angeles.* $3.75 (cloth); $2.75 (paper). viii + 274 pp. + 1 map. 1951.

Ira Waddell Clokey, a mining engineer by profession, devoted a great deal of his life to an avocation of

botanical study. His professional work took him to Colorado and Mexico, where he made extensive collections and careful investigations of the speciation and distribution of the flora. In 1935 he selected the Charleston Mountains of Nevada for intensive botanical research, subsequently devoting the collecting seasons of 1936 to 1940 there, and making shorter visits in 1941 and 1942. The present volume, published posthumously, sets forth the results of this work.

The main part of the book is the flora itself, with keys for identification, nomenclatural synonymy, and citation of specimens. Only generic descriptions are given. The total vascular flora treated includes 699 named entities, 48 of which are considered to be endemic to the Charleston Mountains or to Clark County. An Introduction presents notes on the general geographic and botanical aspects of the region, a history of botanical exploration, the geology of the mountain area (contributed by Chester R. Longwell), physiography and climate, and a brief description of the major plant associations. The Introduction closes with a discussion of endemism and the geographic affinities of the flora. There is an index to the technical names of the plants.

Clokey's book is a "local flora" in the finest meaning of the term. It is based upon abundant material, well collected, preserved, and studied. Specimen vouchers for the entities recognized, though centered at the Herbarium of the University of California, are widely duplicated in other herbaria. The author made full use of assistance from specialists in the proper determination of specimens. Over and above this technical perfection is the author's obvious consciousness of the larger problems involved, and of the probable significance of his work in their eventual solution. Herbert L. Mason, in a Foreword to the book, states this relationship clearly: "Such unit studies of the flora of western North America will play an important part in building the foundation for researches in floristic plant geography that will follow when enough similar detailed works are completed. The many problems of disjunct distributional patterns of species and of the apparent relationship between the flora of the high mountains of southern California and the Rocky Mountains will yield more easily to solution when the details of the floras of the intervening ranges are known."

H. M. RAUP



A REVISION OF THE COLOMBIAN SPECIES OF MONNINA (POLYGALACEAE). *Smithsonian Misc. Coll., Vol. 121, No. 3. Mary Vaux Walcott Fund for Publications in Botany. (Publ. 4100).*

By Ramon Ferreyra. Smithsonian Institution, Washington. 50 cents (paper). v + 58 pp.; ill. 1953.

The author of this paper is Professor of Botany at the University of San Marcos, Lima, Perú, and prepared the work while at the U. S. National Herbarium as a Guggenheim Fellow. *Monnina* is a New World genus distributed chiefly in the Andes of northwestern South America. The author has already published a revision of the Peruvian species, and has in preparation similar studies for those in Ecuador and Venezuela. Such regional treatments are considered advantageous because of the high endemism in the genus. The present paper deals with 32 species, most of which appear to be endemic to Colombia. Eleven of them are new to science. All of the species are illustrated with line drawings of technical characters.

H. M. RAUP



FLORA OF GUATEMALA. *Fieldiana: Botany, Vol. 24, Part III.*

By Paul C. Standley and Julian A. Steyermark. Chicago Natural History Museum, Chicago. $4.50 (paper). v + 432 pp.; ill. 1952.

This volume is Part III of the authors' Flora of Guatemala. It covers the families: Commelinaceae, Pontederiaceae, Juncaceae, Liliaceae, Smilacaceae, Haemodoraceae, Amaryllidaceae, Dioscoreaceae, Iridaceae, Musaceae, Zingiberaceae, Cannaceae, Marantaceae, Burmanniaceae, Casuarinaceae, Piperaceae, Chloranthaceae, Lacistemaceae, Salicaceae, Myricaceae, Juglandaceae, Betulaceae, Fagaceae, and Urticaceae. Like other parts of the work, it contains keys to genera and species, critical taxonomic notes, extensive references to literature and synonymy, habitat notes, data on geographic distribution by Departments in Guatemala, general range outside that state, and detailed descriptions of individual species. Fifty-six species are illustrated with line drawings as text figures. The book contains descriptions of 69 new species, and 7 new nomenclatorial combinations. Most of the new species are in the Piperaceae (*Peperomia*, 20; *Piper*, 43). There are 2 new species of *Juglans* (contributed by Wayne E. Manning), and 4 in the Urticaceae (*Pilea*, 3; *Urera*, 1). Throughout the work the authors have included rather copious and excellent notes on the economic significance of plants wherever such could be defined. Vernacular names are given if they are available. The book closes with an index to generic names.

H. M. RAUP



ORCHIDS OF GUATEMALA. *Fieldiana: Botany, Vol. 26, No. 1.*

By Oakes Ames and Donovan Stewart Correll. Chicago Natural History Museum, Chicago. $4.00 (paper); $5.00 (buckram). xiii + 395 pp.; ill. 1952.

The present volume is the first in a series that will, as

noted in its Preface, be the first comprehensive systematic treatment of all the orchids known to occur in Guatemala and British Honduras. A total of 527 species and 25 varieties, representing 89 genera, will be described in the work as a whole. Most of the research for it was done in the Oakes Ames Herbarium and Library at the Botanical Museum of Harvard University. The late Professor Oakes Ames was the guiding spirit in the project, following the work critically as it was done, and supporting it financially. D. S. Correll did the active research, and states in the Preface that he is personally responsible for the determination of specimens and for the final preparation of the text. Specimens other than those in the Ames Herbarium are cited from the Gray Herbarium, the Herbarium of the Chicago Natural History Museum, the U. S. National Herbarium in Washington, and from the University of Michigan Herbarium. This first volume treats 29 of the genera, and covers the tribes Cypripediloideae, Ophrydoideae, Polychondreae, and the Kerosphaereae through the genus *Epidendrum*.

The Preface contains acknowledgments and an abbreviated account of the history of orchid collections in the region. An Introduction follows, in which there are notes on the evolutionary relationships of the Orchidaceae, their general relations to environment, and their economic significance. A section on geographic distribution makes numerical comparisons of species in the various political subdivisions of Guatemala, and compares the whole orchid flora with that of other parts of Central America. Geographical notes of somewhat more significance are derived from a paper by Standley and Steyermark on "The Vegetation of Guatemala," contained in *Plants and Plant Science in Latin America*, edited by Frans Verdoorn, 1945. Another section contains a brief but concise and well-prepared statement of the "general characteristics of orchids."

The present volume presents keys to all the genera to be treated in the work as a whole. In the treatment of individual genera and species there are keys, detailed descriptions, and notes on habitat, frequency, and general range. There are copious references to the taxonomic literature and synonymy, and extensive citations of specimens. The book is superbly illustrated with drawings representing all of the genera and over 100 additional species. Several artists have contributed drawings, but most of them were done by Blanche Ames (Mrs. Oakes Ames) and Gordon W. Dillon.

H. M. RAUP



PHILIPPINE ORCHIDS. *A Detailed Treatment of Some One Hundred Native Species.*

By Reg S. Davis and Mona Lisa Steiner. The William-Frederick Press, New York. $5.00. xiv + 270 pp.; ill. 1952.

The rich orchid flora of the Philippine Islands has been collected assiduously for over a century, both for botanical study and for commercial purposes. Definitive taxonomic treatments were published by Oakes Ames and E. D. Merrill between 1905 and 1925. There has remained a need, however, for a book that could be used by the host of amateur or professional growers of orchids that has sprung up throughout the world. The present volume should prove useful for this purpose, though it makes no claim to completeness. It deals with only about 100 of the species known to occur in the Philippines, but the authors say that within this number they have included "most of the plants of horticultural importance as well as representatives of the more common genera."

Introductory matter contains notes on the history of orchid collection and study in the Philippines, the geography and climate of the islands, and their general floristic affinities, and finally a brief review of the structure of orchids, the last illustrated with line drawings. Descriptions of genera and species comprise most of the book. They include abundant notes on definitive characteristics, occurrence, phenology, and habitat. One hundred and eight species and varieties are illustrated by excellent half-tone photographs. The book closes with a brief bibliography, a glossary, and an index. It is well printed and bound.

H. M. RAUP



FLORISTIC RELATIONSHIPS BETWEEN EASTERN ASIA AND EASTERN NORTH AMERICA. *Trans. Amer. Philos. Soc., Vol. 42, Part 2.*

By Hui-Lin Li. The American Philosophical Society, Philadelphia. $1.00 (paper). Pp. 371–429; ill. 1952.

I once had the pleasure of watching E. D. Merrill of the Arnold Arboretum name a large and varied collection of plants that had come to that institution from southeastern Asia. The names of genus after genus were familiar, and might have been used on a collection from the Appalachians. The similarity was at once bewildering and challenging. Hui-Lin Li is the latest in a long and illustrious line of students who have taken up the challenge presented by the close relationship of the widely separated floras of eastern Asia and eastern North America. His paper, though it reports but little in the way of new or recent discovery, makes a highly significant contribution merely by bringing up to date and gathering into one publication the results of modern research on the old problem.

The Introduction contains a brief but thorough review of extant literature, with special attention to the "identical species" of the two regions listed by Asa Gray in the latter's classical papers on the subject. The author shows that the similarity in the floras of the two regions is generic, and rarely extends to species.

He decries the continued use of Gray's outmoded lists in recent geographic papers that purport to be based upon modern taxonomic concepts. That Li's own study is soundly based is suggested by his section on acknowledgments. He has had abundant access to the principal herbaria and botanical libraries in America, China, and Formosa. Further, he has had assistance and advice from some of the most astute taxonomists and phytogeographers in this country.

The main body of the paper consists in discussions of the distributional patterns of genera that appear in the two floras, with carefully considered notes on related species. Fifty-nine families are treated, chiefly angiosperms. Range maps are given for 56 of the genera, and an index to all plant names used in the text.

Essential facts about the plants that show disjunctive ranges in eastern Asia and eastern North America are worthy of note. Most of the genera are distinctly of temperate climates or extend into the subtropical. Very few have species that extend into the glaciated regions. As a rule, they have wider ranges in Asia than in America. In Asia there is a notable concentration of the more temperate elements "in China along the Yangtze Valley from Szechuan, through Hupeh and northern Kiangsi, eastward to central Japan." Most of the genera are of woody plants, nearly all of which are deciduous. If herbaceous, they are nearly all perennial with heavy rootstocks. Most of the herbs have only a few large leaves that develop early in spring before they are shaded by the overwood of the forests. The various species within the genera are nearly all "good species," clearly defined taxonomically. A large proportion of the genera belong to families that are generally regarded as structurally primitive in the phylogenetic scale. Most of the woody genera are plants with simple leaves; and most of the species, both woody and herbaceous, are without any special adaptations for dispersal. Although a few of the tree genera contain species that dominate in their respective forests, the majority are relatively rare in occurrence. In both continents, though especially in Asia, they are associated with a large number of endemic ligneous genera. In both areas they occur on land surfaces that probably have not been submerged since the close of the Cretaceous and have not undergone any major surface changes.

Li states finally that these disjunct floras "appear to be the remnants of a great mesophytic forest that extended over all the northern hemisphere and reached the arctic regions in the Tertiary. Geologic changes . . . have destroyed and changed the floras of many lands so that this mesophytic forest of the Tertiary in the northern hemisphere survives mainly in eastern Asia and eastern North America, with only scattered relics in southeastern Europe, western Asia, and western North America." He proposes the term "Tertiaromesophytic" for it, to replace the commonly used "Arctotertiary."

H. M. RAUP

STUDIES OF PACIFIC ISLAND PLANTS. X. THE MELIACEAE OF FIJI, SAMOA AND TONGA. *Contributions from the U. S. National Herbarium, Vol. 30, Part 4. By A. C. Smith. Smithsonian Institution, Washington.* 50 cents (paper). v + Pp. 469–522. 1952.

The author of this paper describes it as a "limited revision" of the Meliaceae for the region concerned, designed to facilitate the identification of the species. A. C. Smith has collected extensively in Fiji, and has been engaged in critical studies of the Pacific Island flora for many years. He has utilized not only his own material, but has visited or borrowed from the principal herbaria of the world. Preceding papers in the series here represented were published in the *Bulletin of the Torrey Botanical Club* and in the *Journal of the Arnold Arboretum* in the years 1941 to 1951. Thirty-six species in the Meliaceae, in 4 genera, are considered to be indigenous to the region (the island groups mentioned in the title, and a few nearby such as Niue, and the Horne and Wallis Islands). Species occurring only in cultivation on these islands are not included. Eleven species and 2 varieties are described as new. The paper contains a key to the 4 genera, keys and descriptions for the species, and an index.

H. M. RAUP



PLANT PHYSIOLOGY

PHYSIOLOGY OF SEEDS. *An Introduction to the Experimental Study of Seed and Germination Problems. By the late William Crocker and Lela V. Barton. The Chronica Botanica Company, Waltham; [Stechert-Hafner, New York.]* $6.50. xviii + 267 pp.; ill. 1953.

This monograph on seed physiology, written by two members of the staff of the Boyce Thompson Institute, is advanced as "an outline, rather than a treatise" of the present knowledge on seeds and germination. Aspects of seed physiology covered include chemical composition, water relations, respiration, germination and dormancy, seed storage, vernalization, embryo culture, metabolic and energy changes accompanying germination, and seed transmission of disease.

The book is oriented for the use of research workers concerned with practical problems of seed production and germination. With this orientation, the presentation of the material is often more descriptive than analytical. The 1100 well chosen references serve to illustrate each point, rather than to exhaust the evidence concerning each topic. *Physiology of Seeds* therefore serves to present the known phenomena of seed physiology in a well organized and documented fashion, to both the student of practical seed production and the more general plant physiologist. The underlying biochemical bases and functions of many of these phenomena, while touched upon briefly, are in fact still

imperfectly understood, so that much more fundamental research must be accomplished before a work of this sort can be written from a more dynamic and analytical point of view.

A. L. JAGENDORF



ECONOMIC BOTANY

PFLANZLICHE INFEKTIONSLEHRE. *Lehrbuch der allgemeinen Pflanzenpathologie fur Biologen, Landwirte, Förster und Pflanzenzüchter.*

By Ernest Gäumann. Verlag Birkhauser, Basel. S. fr. 44.50 (cloth); S. fr. 40.50 (paper). 681 pp.; ill. 1951.

This is the second edition of Gäumann's masterly treatise on the principles of plant pathology, of which the first edition is available in English in Brierley's translation. The first German edition was written during the Second World War and was published in 1946. The English edition appeared in 1950, only a year or so before the publication of the second German edition.

The main reason for this early revisal of the first edition was Gäumann's desire to incorporate in the book suitable examples from the great body of literature published in the decade 1940–1950. Undoubtedly he felt, too, that the original book was actually already out of date on its first appearance, since much of the phytopathological literature that had appeared during the war years was not available to him in his isolation in Switzerland.

Those who have not seen the present edition may wonder to what extent it renders the first one out of date. In this connection, the method of revision is important. The work was revised with a minimum of rewriting. The organization of the work is exactly as before, but many of the examples used in the earlier edition have been eliminated and replaced by more appropriate ones from newer literature. Here and there, the author felt it desirable to rewrite whole subsections. Generally, however, the "summing-up" at the end of each subsection is very little affected by the inclusion of new material. A great amount of new material has been introduced in the form of tables, graphs, and photographic illustrations. As a repository of factual information the new book is therefore a great advance over the old one. Though the book is of value as a storehouse of information, it is infinitely more valuable for its interpretation of the modern research literature of phytopathology; and it is safe to say that no one is better qualified for this task than Professor Gäumann. The gradual transference, over the years, of his interest from the field of mycology to that of the physiology and biochemistry of host–parasite relationships, as exemplified, for instance, in his studies on lycomarasmin, lends increasing value to his interpretations concerning the nature of disease resistance.

The work is so well known through its first edition that any attempt at a general appraisal would be superfluous. It is the major attempt thus far made to build up a theoretical framework for host–parasite relationships. The author theorizes freely, and his hypotheses are always thought-provoking, even if the reader cannot always arrive at identical conclusions.

As for the need of an English translation of the new edition, it may be presumed that the same reasons apply that led to Gäumann's revision. However, the old edition is still a valuable book with much the same general conclusions, even though it lacks some interesting references to recent researches.

T. JOHNSON



PLANT DISEASES. *Second Edition.*

By F. T. Brooks. Geoffrey Cumberlege, Oxford University Press, London, New York, and Toronto. $7.50. xiv + 457 pp.; ill. 1953.

F. T. Brooks, the author of this book, was a student of H. Marshall Ward, the leading plant pathologist in England half a century ago and the author of an unexcelled book, *Disease in Plants* (Macmillan, 1901), in which were brought together the studies of the physiology of plants and the diseases due to the malfunctioning of the normal physiological activities. The first edition of Brooks' *Plant Diseases* appeared in 1928, and the manuscript of the second edition was in the hands of the publishers by December, 1951. The author's demise in March, 1952, left the task of reading the proofs to W. J. Dowson, S. D. Garrett, and N. F. Robertons, former students of the author. The text was not altered but remains as Professor Brooks left it.

The Introduction discusses briefly the losses due to plant diseases, their causes, symptoms, and dissemination, epidemic and sporadic occurrence, susceptibility and resistance to disease, influence of the environment on the incidence of diseases, their control, and legislative regulations designed for their control.

The second chapter discusses rather briefly the diseases not due to parasitic organisms. Virus diseases are discussed in Chapter III, grouped by their host plants. For each disease the symptoms are described briefly, variations in susceptibility of host species, the vectors and, where known, the control.

Chapter IV is devoted to plant diseases caused by bacteria, the nomenclature of the parasite being that of W. J. Dowson in his *Manual of Bacterial Plant Diseases*, although the names used in Bergey's *Manual of Determinative Bacteriology*, 6th ed. are also given if different. It is interesting that the author considers about 20 species of bacteria causing plant diseases to be important enough in Britain to be worthy of mention, aside

from a number of other species causing plant disease in the United States and various tropical and subtropical regions. It is to be feared that the Gulf States in which the citrus canker was so vigorously combatted some years ago will feel hurt in not being included (as is South Africa) among the regions where this disease was eradicated.

The plant diseases due to Actinomycetes are the subject of a short chapter, the various forms of potato scab being given the main attention. Chapter VI, on the Plasmodiophorales, concerns itself, mainly, with *Plasmodiophora brassicae* and *Spongospora subterranea*. Chapter VII contains a key to the orders of the true fungi, most of those orders being omitted in which no plant pathogens are recognized. Chapters VIII to XII are devoted to the diseases caused by Ascomycetes, Chapter XIII to the Ustilaginales, XIV to the Uredinales, and the next three to the remainder of the Basidiomycetes.

The diseases caused by the Fungi Imperfecti (Deuteromycetes) are discussed in three chapters, one chapter is devoted to *Cephaleuros*, a green alga, and the final chapter takes up the fungicides.

Although primarily written for readers in Great Britain, the more outstanding plant diseases of the other Commonwealth nations are included, with a considerable number of those of the United States, even many that do not occur in British areas of the world. Naturally the bibliographical references at the close of each chapter are mainly British or from other European sources, but a generous proportion of North American publications is included. It is refreshing to note that these bibliographical references are not, as might be feared, the old ones. They are surprisingly up to date. Thus 37.5 per cent of those for the Fungi Imperfecti date within the last ten years before the book went to press, and for the last twenty years the percentage is 69. For the more recent subject of virus diseases these figures are respectively 66 and 93 per cent.

To an American the use of the name *Cystopus* instead of the more familiar *Albugo* seems strange. Another seeming oddity is the inclusion of the species of *Botrytis*, whose perfect, presumably apothecial stage is still unknown, among the Sclerotiniaceae; but at second thought, this seems more logical than to defer their discussion to the chapter on Moniliales. *Cyttaria* is included among the inoperculate Discomycetes in the Order Helotiales. Very recent studies by N. H. White have indicated that this genus belongs in the Pezizales (i.e., among operculate forms).

The illustrations are not numerous, but with few exceptions are very good. Although not written primarily for American students of plant diseases, this book is one that plant pathologists in this country should have at hand.

ERNST A. BESSEY

PLANT DISEASES *in Orchard, Nursery and Garden Crops. By Ernst Gram and Anna Weber; edited and adapted by R. W. G. Dennis; translated by Evelyn Ramsden. Philosophical Library, New York; [MacDonald, London.]* $18.50. 618 pp. + 10 pl.; text ill. 1953.

This offering of workers at the State Plant Pathological Experiment Station, Lyngby, Denmark, has passed through two earlier editions in the Danish language. It is intended for the practical grower, not the academician. As such, the gross symptoms of the various diseases receive emphasis, and the book is practically devoid of the customary microscopic details of parasite morphology in diseased tissues. There are five sections, of which the first deals with the general nature of plant diseases and the concluding one with principles of disease control. The main body of the work is in three sections, dealing respectively with diseases of fruits, vegetables, and ornamental plants. The various diseases are grouped according to the host attacked. Perhaps the distinctive feature of the book may be said to be the keys for diagnosis of the diseases of a given host according to symptoms and the portion of the plant involved. The book is well illustrated, documented, and indexed, and the publishers are to be commended for a high order of workmanship in the production of this fine volume.

FREDERICK T. WOLF



DISEASES OF VEGETABLE CROPS. *By John Charles Walker. McGraw-Hill Book Company: New York, Toronto, & London.* $7.50. x + 529 pp.; ill. 1952.

This excellent book "is the outgrowth of a lithoprinted manual published originally by the author in 1939 for use in a course in vegetable diseases offered to graduate students." It has been brought up to date, the Preface being dated December, 1951.

The subject matter is divided into 16 chapters concerned with the diseases of special vegetable crops or groups of related crops. These are: asparagus; bean and lima bean; beet and chard; carrot and parsnip; celery and parsley; crucifers; cucurbits; lettuce, endive, escarole, chicory, salsify, and globe artichoke; onion, garlic, leek, chive and shallot; pea; pepper and eggplant; potato; rhubarb; spinach; sweet potato; tomato. In each chapter the diseases are discussed under various headings such as non-parasitic diseases; those due to bacteria, damping off, diseases incited by phycomycetes, powdery mildews, leaf spots, root-rots, wilts, anthracnose, rots of the fruits, rusts, nematodes, and the various types of virus-incited troubles, etc. Under each classification there follow the bibliographic references. Where a disease, e.g., *Sclerotinia*, is common to various groups of hosts it is given a full discussion under one host, and reference thereto is made from the sections on

other affected hosts. Each disease is described by symptoms, causal organisms, disease cycle, and control. Especial attention is given to diseases caused by viruses. The use of resistant strains for control of diseases is emphasized where such strains are available.

The book is up to date, as evinced by the numerous bibliographical references to publications in 1950 and to some few in 1951. It is not burdened with old references except where these are fundamental, as, for example, some of the publications by E. F. Smith, before 1900.

There is a very gratifying freedom from typographical errors, except a few cases in the index where Latin names are misspelled. I wonder why a minor rot of the tomato (p. 466) is ascribed to *Basisporium* when *Nigrospora* seems to be the correct name of the genus.

The illustrations are well chosen and excellent. This book should prove to be very valuable for students, teachers, agricultural county agents, and for such growers of vegetable crops as can understand plain English and follow the directions given for their control.

ERNST A. BESSEY



FOREST MANAGEMENT.

By H. Arthur Meyer, Arthur B. Recknagel and Donald D. Stevenson. The Ronald Press Company, New York. $6.00. xii + 290 pp.; ill. 1953.

This is an excellent new textbook which appears to be well designed for a single term course in forest management. The authors make no effort to review or discuss the fields of silviculture, forest engineering, protection, etc. Such restrictive treatment serves to delimit the field of forest management, and places emphasis on the fact that forest problems on the management level are concerned primarily with the organized application of available silvicultural and related knowledge, rather than with the pursuit of such knowledge. The book is divided into four parts. The first deals with the history, scope, objectives, and present status of forest management; the second, with surveys, maps, growing stock, growth, and other techniques and details concerned with the general organization of a forest property for management. Part Three is concerned with regulation and a discussion of the normal forest. Part Four is devoted to a study of the principles and contents of management plans for small, medium, and large forests. Various well selected specimen plans are included and discussed.

SCOTT S. PAULEY



GENERAL AND SYSTEMATIC ZOOLOGY

A GENERAL ZOOLOGY OF THE INVERTEBRATES. *Third Edition.*

By G. S. Carter; foreword by Julian S. Huxley. Sidgwick & Jackson, London; [The Macmillan Company, New York]. $5.75. xxv + 421 pp. + 13 pl.; text ill. 1951.

As stated by the author, "this book is in no sense a text-book of invertebrate zoology." Rather, it is a theoretical treatise on the principles and problems of animal biology, in which representatives of the invertebrate phyla are employed as illustrative material. As compared with the vertebrates, the invertebrates manifest great diversity in morphology, in development, and in their physiological processes; thus they provide a far more extensive field for comparative study. The book comprises four sections: (1) protoplasm and the free-living cell; (2) the multicellular body, the origin and organization of the Metazoa; (3) comparative physiology of representative organisms; and (4) life histories, behavior, and habits among the invertebrates. It closes with a discussion of the evolution of the invertebrates, and a list of books and articles for further reading.

The book begins with a discussion of the chemical and physical properties of protoplasm, its organization into cells, colonies, syncytia, tissues, and the further integration into the organs and organ systems of higher invertebrates. Major consideration is given to the maintenance of the integrity of the individual and the manner in which specificity is imposed on the constituent units throughout those changes which occur during the life cycle. Evidence is presented to show that specific organizations during development, metamorphosis, regeneration, and transplantation is effected by quantitatively graded metabolic processes that take place in axial fields, and that these gradients maintain the unity of the organism as a whole. Throughout the progressive levels of morphological and physiological organization, there is a general increase in the complexity and efficiency of physiological processes. The problems of development, alternation of generations, the significance of larval types and of metamorphosis are well presented. Types of behavior are correlated with progressive development of the sense organs and the integrative capacity of the nervous system. Adjustment to environment and ecological relations are based on responses to stimuli. There is no consideration of genetics, since the author believes that that subject has been well summarized in several recent books.

The invertebrates are represented as a series of major patterns of organization, derived from a single animal stock, and adapted in different ways to secure evolutionary advance. The factors which have operated to enhance or retard progress are considered. The book is well written, adequately illustrated, and forms a stimulating contribution to the literature of invertebrate zoology.

HORACE W. STUNKARD

THE BUTTERFLIES OF VIRGINIA. *Smithsonian Misc. Coll., Vol. 116, No. 7. [Publ. 4050].*

By Austin H. Clark and Leila F. Clark. The Smithsonian Institution, Washington. $2.25 (paper). viii + 239 pp. + 1 pl. + 1 folded map; text ill. 1951.

This monographic work by Austin H. Clark (Curator Emeritus of Echinoderms) and Mrs. Clark (Librarian) of the Smithsonian Institution is the result of 33 years of extracurricular interests of the authors. During this time they have intensively collected, observed, and studied the butterflies of Virginia and the District of Columbia, having collected personally in more than 800 localities and visited each of the 100 counties of Virginia at least twice. It is not surprising, therefore, that this book is the most thorough local study of butterflies ever published in North America; or that because of the Clarks' efforts the butterflies of Virginia and the District of Columbia (of which latter region the butterflies were monographed by A. H. Clark in 1932) are now as well, or better, known as those of any comparable regions in North America. This is of great scientific significance, for it is only when the study of a group has reached such an advanced stage as this that we are able to formulate generalizations with any degree of confidence.

This book will be especially useful to students of distribution, not only because of its completeness but also because of the strategic position of Virginia and the wealth of zones and environments found in the State. The largest part of the area is Upper Austral Zone, but there is much Lower Austral in the southeastern part. The hilly and mountainous areas westward, above 1,500–2,000 feet are Transition Zone; and a few isolated areas above 4,000 feet are Canadian Zone, containing some characteristic butterflies.

A total of 154 species and subspecies are listed (only 147 have been recorded from North Carolina and 132 from New York, which is probably the best known eastern state after Virginia) and characterized in keys to family, subfamily, genus, and species. All are illustrated by excellent photographs, often of the under sides as well as the upper sides. There are thorough discussions of the variation, range within the state, ecology, biology, and phenology of most of the species. There is a lengthy discussion of the geographic, topographic, and sexual variation of *Papilio glaucus* L. which will be of great interest to all students of variation. A very full discussion of the status of *Colias philodice* Godart and *C. eurytheme* Boisduval is likewise of particular interest because of the recent invasion of the range of the former by the latter, with the consequent appearance of large hybrid populations.

ALEXANDER B. KLOTS



THE AMPHIBIANS OF THE SOLOMON ISLANDS. *Bull. Mus. comp. Zool., 107, No. 1.*

By Walter C. Brown. Museum of Comparative Zoology at Harvard College, Cambridge. $1.00 (paper). 64 pp. + 8 pl.; text ill. 1952.

A systematic review of the amphibians of the Solomon Islands. The fauna of these islands, as discussed by Brown, consists of 1 toad, 2 tree-frogs, and 15 true frogs. Much of the material on which this paper is bases was collected by men in service.

It is interesting to note that when Boulenger described the amphibians of the Solomons in 1886, he recognized 9 species and suggested that the fauna was probably well known. Brown, with twice as many validated species, has reached an opposite conclusion, and feels that there is still a tremendous amount to be learned about the amphibians of the Solomon Islands.

ARNOLD B. GROBMAN



ECONOMIC ZOOLOGY

FISHERY SCIENCE. *Its Methods and Applications.*

By George A. Rounsefell and W. Harry Everhart. John Wiley & Sons, New York; [Chapman & Hall London.] $7.50. xii + 444 pp. + 3 pl. + 1 folded map; text ill. 1953.

A comprehensive textbook of fishery science has long been needed, and this might be called "installment two" of such a work. The authors do not claim that this is a guide to ichthyology or a treatise on biology, but emphasize that it is primarily about methods. They also say that the real purpose of the book is to present the problems of fisheries and to show what methods may be used to solve them. Problems, however, are presented in the final chapter, and seem to be lost sight of in the main part of the book. If the authors had adhered to their "real purpose," this would have been a very different book, but as it is the end is too often lost sight of in the consideration of the means. A presentation of the problems of fisheries would require some ideas about the basic ecological principles which are the concern of fisheries, and we find few such ideas here. Installment one, therefore, remains to be done. Whoever attempts it could do far worse than consult Johnstone's *Conditions of Life in the Sea*, a book that influenced an entire generation of British fisheries workers, and one of the few satisfactory textbooks of fisheries biology.

Fishery Science is nevertheless a very useful compilation of all sorts of fisheries techniques, for both fresh and salt water, from stream improvement, tagging, gear, and the like, to statistical methods. It is good to have all this material brought together in one place, even if the mechanical arrangement of sections makes the reading rather choppy at times. We only hope that instructors who use this as a textbook will point out that there are still other methods and pro-

cedures not mentioned by the authors, and that the student will have the necessary biological and statistical background to fill in the gaps and evaluate the techniques. Occasionally the treatment is too condensed, and some topics are mentioned only to be laid aside, while in other cases they are omitted altogether. Many of these oversights will probably be corrected in future editions.

JOEL W. HEDGPETH



MARINE GAME FISHES OF THE WORLD.

By Francesca La Monte; illustrations by Janet Roemhild. Doubleday & Company, Garden City. $3.50. 190 pp.; ill. 1952.

This is a book for marine anglers, where ever they might be, with an emphasis on information for the fisherman rather than on ichthyological data. Of the many game species described, 138 are well illustrated in color or in black and white, and each is described as to common and scientific name, distribution, color, identifying characteristics, size, food, habits, and edibility, together with angling hints. Grouping of the species is generally phylogenetic, beginning with the sharks and rays, and with only occasional deviations for convenience. Only the salmon, as a group, are missing, but this is understandable from the angler's point of view, since these are regarded as freshwater species. International game-fish records are listed, and for the wandering angler an excellent geographical section is provided which deals with fishing seasons, accommodations, and the availability of boats, guides, and tackle. All in all, this is a fine, compact book, uncluttered but rich in information.

C. P. SWANSON



TROPICAL FISH AS A HOBBY. *A Guide to Selection, Care, and Breeding.*

By Herbert R. Axelrod; with two chapters by Myron Gordon and one chapter by James W. Atz. McGraw-Hill Book Company, New York, London, and Toronto. $4.00. xvi + 264 pp.; ill. 1952.

Far more than half of this handsome volume deals with the various kinds of tropical fish, and details their habits—particularly activities related to breeding. For convenience they are divided into live-bearers and egg-layers, with catch-all chapters on scavengers—both fish and invertebrate—and plants. A handy appendix summarizes the various types of fish described under headings of popular name, scientific name, source, type of reproduction, temperature requirements, disposition, and facts on breeding. Contributed chapters, How Fish Get their Names (Myron Gordon), Aquarium Genetics (Myron Gordon), and The Balanced Aquarium Myth (James W. Atz) add practical information that supplement chapters on the maintenance of a healthy aquarium and care for the gadgetry needed in temperature control and aeration.

LORUS J. & MARGERY J. MILNE



DISEASES OF POULTRY. *Third Edition.*

Edited by H. E. Biester and L. H. Schwarte. The Iowa State College Press, Ames. $11.50. xiii + 1245 pp. + 2 pl.; text ill. 1952.

Veterinarians, pathologists, and workers in fields related to poultry husbandry will welcome this volume, the 3rd edition of a textbook originally published in 1943. Recent advances in the various phases of poultry disease are discussed in the volume by 35 contributors who are experts in their respective fields. As in the previous editions, the major consideration relates to the recognition, control, and prevention of the many diseases that affect poultry. Considerable information is also presented, however, regarding the anatomy, digestion, hematology, and nutrition of poultry. Thus, the book will be of much use to workers in many subjects allied to poultry science.

R. VAN REEN



THE CLASSIFICATION OF WEST AFRICAN LIVESTOCK. *Technical Communication No. 7 of the Commonwealth Bureau of Animal Breeding and Genetics.*

By I. L. Mason. Commonwealth Agricultural Bureaux; Farnham Royal, Slough, Bucks. 10s. 6d. vii + 38 pp. + 20 pl. + 1 folded map. 1951.

The purpose of this book is to provide specialists in animal breeding with a brief description and classification of the many types of livestock which are found in West Africa. This has been done, most concisely, by means of verbal description and the use of 38 excellent photographs. The author, using a method which indicates their relationship to the breeds in surrounding areas, has classified the local breeds and types of cattle, horses, sheep, and goats. The existence of 22 types of cattle in West Africa complicates the task of classification. The author's classification, based largely upon hump and horn form, divides these 22 types into 4 major groups, the largest of which is the Humped Cattle (Zebus), which is made up of 12 types and four subgroups. When available, recent references giving further information regarding the livestock types are cited. This book should be of special value to those interested in crossbreeding and in the adaptation of types of animals to a tropical environment.

FREDERICK N. ANDREWS

ANIMAL GROWTH AND DEVELOPMENT

DIE ENTWICKLUNG DES BRAUNEN GRASFROSCHES RANA FUSCA ROESEL *dargestellt in der Art der Normentafeln zur Entwicklungsgeschichte der Wirbeltiere.*

By Fr. Kopsch. Georg Thieme Verlag, Stuttgart [Grune & Stratton, New York]. DM. 48.00. vii + 70 pp. + 2 pl.; text ill. 1952.

This work follows in plan and format the "Normentafeln" for Vertebrates by Keibel, which have apparently been discontinued. *Rana fusca*, the common European grass frog, is as widely used for experimental research in Europe as *Rana pipiens* in this country. Its development is subdivided into 30 stages as follows: cleavage, 1–3; gastrulation, 4–6; neurulation, 7–9; embryonic period, 10–17; larval period, 18–26; metamorphosis, 27–30. Detailed descriptions of each organ are given in a tabulated form for each stage, following the pattern of Keibel's tables. The drawings illustrating the external features of the different stages are done, in part, by Lisbeth Krause, who is known to all American embryologists for her beautiful illustrations of Harrison's stage series of *Amblystoma*, and in part by F. W. Müller. A general chapter summarizes and integrates the organogenesis of the different organs.

The scope of the work is enlarged, and its usefulness considerably enhanced, by the addition of two chapters. One of these gives a detailed comparison of *Rana fusca* with the closely related species, *Rana arvalis*, and includes a wealth of morphological and ecological data. In the other chapter, the distinguishing characteristics of all European anuran larvae are tabulated, and their identification is facilitated by drawings of the horny jaws and suckers. Altogether, the book will be a valuable companion for European embryologists. Unfortunately, the bibliography had to be omitted for reasons of economy.

The only criticism which one may raise concerns the choice of the stages. This is always an arbitrary matter, but in the present case it is regrettable that the author did not adapt his stages to Shumway's widely adopted stage series of the very similar American frog, *Rana pipiens*, and to that of *Rana sylvatica* by Pollister and Moore. This could easily have been done by adding a few embryonic stages, and it would have been a helpful step towards a badly needed unification of amphibian series.

VIKTOR HAMBURGER



POST-EGG PERIOD IN ALBATROSSES. *Biological Monographs, No. 4. Nuffield Publication, No. 1.*

By L. E. Richdale. The Otago Daily Times and Witness Newspapers Co., Dunedin. 30 s. 166 pp. + 16 pl.; text ill. 1952.

It is not surprising that the albatrosses have always stirred the imagination of man and that they have been referred to repeatedly in history, fiction, and poetry. As a result, fact and fiction have become blended, and the ornithologist has had to wait a long time to accumulate sufficient information of an accurate nature to enable him to separate the one from the other. In no small measure this information has been gathered by the patient and persistent efforts of the present writer, whose studies have revealed so much concerning the life history of these birds. The present volume is a sequel to an earlier publication, *The Pre-egg Stage in the Albatross Family* (*Q. R. B.*, 25: 340. 1950). It deals primarily with the Royal Albatross, which was studied at Taiaroa Head on the Otago Peninsula, New Zealand. The study covers 16 seasons, from 1936 through 1952, and is concerned with the post-egg period, which begins with the laying of the egg and ends with the departure of the fledgling from the breeding area.

It would be difficult to mention all the observations and conclusions made by the writer in this review. Some will be briefly noted. Both sexes incubate, the male frequently taking charge soon after the egg is laid. The span of time spent on the egg is on the average 6.4 days (range, 1 to 17 days). The incubation period is relatively long, on the average 79.3 days. For approximately 40 days the chick is guarded, and then the attentive spans shorten until the chick is ultimately left unguarded. When about 236 days old (216 to 252) the chick leaves the breeding area and flies off to sea. This long unguarded period has given rise to a persistent legend that the parents completely abandon their offspring, which was then supposed to survive solely on its own fat—the so-called starvation period. Although this idea has been challenged, it still occurs in the present-day literature. Richdale traces the history of this belief and then proceeds to demolish the whole idea with detailed observations, including a photograph of a 226-day-old chick being fed by its parent. From age 40 to 100 days, the chick is fed for 48% of the days, from 100 to 200 days for 79%, and during the last 31 days, for 55%. Let us hope that the starvation period in albatrosses has been laid to rest permanently.

Adolescent sterility seems to occur, inasmuch as females first returning to the breeding ground are "unattached," and although coition may take place, actual successful breeding may not occur for several seasons. Of chicks reared on the peninsula, 6 have returned to the place of hatching at ages 4 to 8 years, but the first female to breed was 9 years old. Although the age structure of the population cannot be ascertained definitely, the oldest alabatross is known to be at least 25 years old, and the average age of the 19 breeding birds is at least 17¼ years. Although the Royal Albatross is the species about which most information is made available, continuous comparison is made, in a thorough critical manner, to other species wherever data are available from the literature, per-

sonal observation, or correspondence. The detailed presentation of the writer's material makes it possible for anyone to evaluate all the conclusions that have been drawn. It is needless to point out that this report, and its companion volume, are necessities for any student of albatross biology.

HENRI C. SEIBERT



ANIMAL MORPHOLOGY

THE PRINCIPAL NERVOUS PATHWAYS. *Neurological Charts and Schemas With Explanatory Notes. Fourth Edition.*

By Andrew Theodore Rasmussen. The MacMillan Company, New York. $4.50. ix + 73 pp.; ill. 1952.

Since the appearance of the first edition in 1932 this excellent set of neuroanatomical drawings, with running text, has been justly famous. Its traditional accuracy and clarity has been carried into the 4th edition. The format is the same, changes prompted by the last 7 years of neuroanatomical research not being radical. Notable are the omission of the olivospinal tract, location of the cortical center for taste in the lower part of the postcentral gyrus and a more extensive origin for the corticopontine fibers.

This volume and the *Atlas of Cross Section Anatomy of the Brain*, which combined some new Rasmussen drawings with the celebrated Villiger-Ludwig brainstem series, constitute a concentrated wealth of material. The Villiger-Ludwig-Rasmussen drawings deal with the pure anatomy of the central nervous system and the present volume with the organization of the nervous system from the practical functional viewpoint. In no other field of basic medical science is the subject material so succinctly presented. Rasmussen's book is recommended without reservation as the work of a great scholar and beloved teacher.

F. N. LOW



ANATOMY OF THE AUTONOMIC NERVOUS SYSTEM.

By G. A. G. Mitchell; Foreword by Sir James Learmonth. E. & S. Livingstone, Edinburgh and London; [The Williams & Wilkins Company, Baltimore]. $10.00. xvi + 356 pp.; ill. 1953.

This book is a welcome addition to the inadequate literature on the autonomic nervous system. There is scarcely a field in modern medical science which is not concerned to a significant degree with the form and function of this system. But, at the risk of overworking superlatives (and tempers), it is suggested that the autonomic nervous system is the one we discuss the most, understand the least, and teach the worst. It is certainly the most difficult to interpret. Current interpretation, confirming time-honored usage, represents it as a double efferent visceral innervation, largely peripheral, and not under control of the will. But a more inclusive concept is necessary in the light of modern knowledge. A system of afferent fibers, double as are the efferent ones, is so intimately concerned with autonomic function that it cannot be ignored. Furthermore, visceral pathways in the central nervous system tend to be dispersed rather than discrete and have been difficult to trace. As a result, the autonomic nervous system has come to be thought of as primarily peripheral, an unfortunate conception. Our information about visceral connections in the higher brain centers is still fragmentary but nonetheless merits inclusion. A thorough exposition of the autonomic nervous system as we know it today is bound to be less concise than most anatomical descriptions, but that is better than incompleteness.

Mitchell follows the more inclusive concept of the autonomic nervous system indicated above. He is well qualified for his task and has handled his material in a manner that should make his book the work of choice in the field. A number of chapters are devoted to autonomic connections in the central nervous system, particularly in the higher centers. More than half of the book deals with the peripheral portion. The text is clearly written and is as factual as the background permits. Controversial interpretation is in general omitted. Within the rather broad framework of original selection of material Mitchell's presentation is praiseworthy. It should be in the library of everyone interested in the autonomic nervous system.

F. N. LOW



ANIMAL PHYSIOLOGY

ANNUAL REVIEW OF PHYSIOLOGY. *Volume 15.*

Edited by Victor E. Hall; Associate Editors, Jefferson M. Crismon and Arthur C. Giese. Annual Reviews and The American Physiological Society, Stanford. $6.00. x + 558 pp. + 1 pl.; text ill. 1953.

This volume continues its reputation of presenting the most detailed and broad coverage of all physiological literature. At the same time the Editorial Committee is encouraging reviewers to be critical in terms of the bias of their own specialties. The latter trend has expanded noticeably in this issue. This seems to add sparkle to the style of several chapters.

The esteemed Dr. Anton J. Carlson was chosen to prepare the innovation of recent years, the Prefatory Chapter. Unfortunately his varied activities left neither time nor energy to prepare the essay, and younger physiologists will miss his valued exhortations. His firm portrait is there: a symbol, to those who know him, of what might have been written.

In listing topics and authors, it will be useful to indicate how many years' literature are covered by each review. Regardless of the number of years considered the most recent journal issues cited will have arrived at the reviewer's library no later than June 1, 1952. Thus, calendar coverage is indicated as follows: "1 yr.," June 1951–June 1952: "2 yr.," June 1950–June 1952; and so forth. The number of articles cited is indicated by the notation: "Refs., 188."

The topics and reviewers: Transport through Biological Membranes (H. H. Ussing; 2 yr.; Refs., 188); Developmental Physiology (N. T. Spratt, Jr.; 2 yr.; Refs., 239); Electrical Activity of the Brain (B. R. Kaada; 2 yr.; Refs., 265); Water Metabolism (N. M. Keith; 1 year.; Refs., 138); Respiratory System (M. Nielsen and E. Asmussen; 1 yr.; Refs., 178); The Digestive System (C. F. Code; 2 yr.; Refs., 222); The Innervation of Skeletal Muscle (R. Hodes; new coverage; Refs., 167); Blood Volume Maintenance and Regulation (I. S. Ravdin, J. M. Walker, and J. E. Rhoads; 2 yr.; Refs., 198); Blood: Formed Elements (T. F. Dougherty and J. H. Dougherty; 4 yr.; Refs., 167); Peripheral Circulation (A. C. Burton; 1 yr.; Refs., 221); Heart (A. P. Fishman and A. Cournand; 1 yr.; Refs., 401); Excitation and Conduction in the Nervous System (M. G. Larrabee and C. Edwards; 1 yr.; Refs., 183); Somatic Functions of the Central Nervous System (J. F. Fulton; 2 yr.; Refs., 133); Visceral Functions of the Nervous System (S. C. Wang; 1 yr.; Refs., 200); Special Senses: Thermal Receptors (Y. Zotterman; new coverage; Refs., 66); Physiology of Vision (H.-T. Chang; 4 yr.; Refs., 199); The Anterior Pituitary and Adrenal Cortex (F. L. Engel; 1–2 yr.; Refs., 316); Reproduction (P. L. Krohn and S. Zuckerman; 1 yr.; Refs., 279); Comparative Physiology of Invertebrate Endocrines (B. V. Scharrer; new coverage; Refs., 187); Liver (F. C. Mann and F. D. Mann; 2 yr.; Refs., 155); and Higher Functions of the Nervous System (H. F. Harlow; new coverage; Refs., 53).

W. S. WILDE



THE MACHINERY OF THE BODY. *Fourth Edition.* *By Anton J. Carlson and Victor Johnson. The University of Chicago Press, Chicago.* $5.50. xxii + 663 pp.; ill. 1953.

Through the addition of two dozen pages (and a price increase of $1.00), this standard introduction to human physiology has received its "most comprehensive revision since its original publication in 1937." Body responses to atom-bomb explosions and the use of radioactive isotopes in research, antibiotics and their limitations, blood banks and gamma globulin, vitamin B_{12}, and biological warfare all receive comment that fits them into the more modern version of the human systems in action. A few new illustrations are welcome. No doubt the retention of so many "production stills" from the University of Chicago teaching films on physiology has a value in classes where these films are shown. Repetition is a good teacher and many of these diagrams, animations, and actual photographs are excellent portrayals of the living process.

LORUS J. & MARGERY J. MILNE



THE LIVING BRAIN.

By W. Grey Walter. W. W. Norton & Company, New York. $3.95. 311 pp. + 3 pl.; text ill. 1953.

This book discusses for the general reader the "mechanism of mind," with emphasis on electroencephalographic studies of sensory perception, attention, pathological conditions, and personality. An account of the evolution of the brain is introduced as a background for this discussion.

The author also describes the interesting "electromechanical creatures" which he has designed and built. The animal properties shown by these beasts include exploration of the environment, phototropism, dodging of obstacles, seeking of food in response to hunger (the creature plugs itself into a battery charger), and the establishment of conditioned responses. The mechanism for this last property was designed on the basis of a simple mathematical model of conditioning.

The appendices describe an electrical working model of nerve, with neon tubes as excitable elements, and electronic circuits for the electromechanical creatures.

The reader may be discouraged by the condensed style of the first chapter, and Figures 1 and 6 are not very clearly explained. Otherwise, this is a readable though somewhat discursive popularization of certain modern approaches to the little-understood subject of cerebral function.

RICHARD FITZHUGH



THE ELECTRICAL ACTIVITY OF THE NERVOUS SYSTEM. *A Textbook for Students.*

By Mary A. B. Brazier. The MacMillan Company, New York. $5.00. x + 220 pp.; ill. 1951.

This book is a direct, well-organized survey of the electrically measurable characteristics of nervous activity. Eighteen brief chapters, each with illustrations and a bibliography, cover a broad range of material in few more than 200 pages. Maintaining a reasonable balance of emphasis, the author devotes approximately one-third of the book to a consideration of excitation and conduction in peripheral nerve, one-fourth to the sense organs and activity in sensory nerves, and the remainder of the book to electrical manifestations of activity in the complex structures of the central nervous

system, including 3 chapters relating to electroencephalography.

The book is the only recent work in English bringing together material from these related fields, each of considerable and growing extent. It is disappointing that the author and publishers have chosen to produce so brief a book. A large portion of any book pitched at the introductory level consists of citations of one fact after another. The author has quite skilfully managed her task in this regard and has written a readable and informative text. Perhaps the chief merit of the book is its organization. It should serve adequately to orient the initiated and it will pleasantly remind workers in the various areas of their value to and of their dependence upon their fellows in adjacent fields.

It is unfortunate that specific bibliographic references do not appear in the body of the text. Both the student and the professional reader often wish to hunt down the bases for quoted conclusions and the detail of some author's enlightened speculation. Occasionally they may even want to verify the citation of observations or resolve ambiguities arising from too cursory generalizations. Success in hunting is here often difficult or impossible, even though almost one-seventh of the the book is bibliography.

Several faults of varying minor degree detract from the over-all quality of the book. The worst of those noticed is a serious misquotation of an experiment in vision (p. 151). Several figures and a table are incompletely labelled or mislabelled. The bibliography might have been more carefully read in proof. Brevity in some instances has resulted in statements either ambiguous or misleading—to say nothing of their being incomplete. One sentence, "This structure can be clearly seen with polarized light through the ultramicroscope," perhaps bears out a statement in the Preface that the book is not intended to be a technical manual. The book is expensive.

C. M. CONNELLY



PROBLEMS IN CEREBELLAR PHYSIOLOGY.
By H. Moruzzi. Charles C Thomas, Springfield, Ill. $3.25. iv + 116 pp.; ill. 1950.

Moruzzi's contributions to neurophysiology, and more particularly to the physiology of the cerebellum, have been many. In this important little monograph he reviews the recent investigations devoted to the anterior lobe of the cerebellum. Of necessity this involves discussion of some terminology—some clarification of the relationships of paleocerebellum, archicerebellum, and neocerebellum—as well as of the role of the cerebellum in autonomic activity and in postural mechanisms. The discussion integrates, in so far as it can at this time, the interrelationships of the cerebellum with the spinal cord, bulbar reticular formation, diencephalon, and cerebral cortex. Although fully realizing the limitations of present information concerning these relationships as well as regarding the possible role played by cerebellar areas other than the anterior lobe, the author is able to come to some general conclusions about these problems and the paths for future research. This small volume will be welcomed by all investigators in this field.

R. G. GRENELL



THE NATURE AND SIGNIFICANCE OF THE ANTIBODY RESPONSE. *Symposium Held at the New York Academy of Medicine, March 21 and 22, 1951. Edited by A. M. Pappenheimer, Jr. Columbia University Press, New York.* $5.00. x + 227 pp.; ill. 1953.

Fourteen papers presented at the conference are included. These deal with theories and sites of antibody formation, the response of immunized animals to stimuli, factors affecting antibody response and the persistence of antibodies in man after immunization, the problem of unity vs. diversity of antibodies, the concept of "valence" of antibodies, experimental production of skin-sensitizing antibodies, allergy and resistance to insulin, immunological reactions mediated through cells, the fate of I^{131}-labeled gamma globulin in rabbits and the fate of injected protein antigens, the localization of antigen in cells by fluorescent-labeled antibody, and a general discussion of radioactive tracers in the study of anti-tissue antibody.

Each chapter has been written by a worker in the specific field and has been well documented. The volume represents a useful contribution to the medical sciences.

C. JELLEFF CARR



ANIMAL NUTRITION

BIBLIOGRAPHY OF THE LITERATURE ON THE MINOR ELEMENTS AND THEIR RELATION TO PLANT AND ANIMAL NUTRITION. *Fourth Edition. Volume III. Compiled and published by the Chilean Nitrate Educational Bureau, New York.* Free upon request. 117 pp. 1953.

The present volume abstracts approximately 1000 articles covering the period from January 1951 to December 1952, and the usual complete indices are provided. As in previous volumes, the abstracts are largely derived from *Chemical Abstracts* and from *Soils and Fertilizers*, a publication of the Imperial Bureau of Soil Science, England. The inclusiveness of the volume is therefore largely determined by the inclusiveness of its sources. A check reveals the omission of a number of important references.

NUTRITION AND DIET THERAPY *in Relation to Nursing.* *By Marie V. Krause. W. B. Saunders Company, Philadelphia and London.* $4.25. x + 562 pp.; ill. 1952.

This book is devoted essentially to the field of dietetics, with particular attention paid to the application of the principles of nutrition to the nursing profession. The volume is divided into four parts: Nutrition and Foods; Diet Therapy; Nutrition in Pregnancy, Lactation, Infancy, and Childhood; and Food Selection, Cookery Rules, and Service. It might have been more satisfactory if the author had omitted the section on nutrition and foods, which presumably is devoted to basic nutrition. The chapters in this section make no reference to the function of zinc in carbonic anhydrase, of pantothenic acid in coenzyme A, or of the functioning of pyridoxine and folic acid. An appendix is provided giving the composition of common foods and the recommended dietary allowances of the Food and Nutrition Board of the National Research Council.

R. VAN REEN



BIOCHEMISTRY

MAN: THE CHEMICAL MACHINE. *By Ernest Borek. Columbia University Press, New York.* $3.00. xi + 219 pp. 1952.

This book is an account by a biochemist of ideas and views of biochemists about the nature of their task and craft. It claims to be the first of its kind, and therefore should repay careful study. It seeks to be intelligible to the general public, and this may be conceded, as well as that the author's heart is in the right place, and that he frequently makes statements with which one may agree. But it is also full of things that fill one with dismay, and even at times resentment. The author is not at all free from at least one quirk of those Sunday Supplementeers whom he ridicules in the Preface: which is to color things black or white, but never intermediate shades. For example, it is proper to extol the achievement of Wöhler in synthesizing urea, but not at the expense of his predecessors. To suggest that these experimental scientists "halted with awe and impotence before a living thing" is not only absurd, but bad history. A DeGraaf cannulating the pancreatic duct of a living dog, and tasting the alkalinity of the fluid; a Sacho analyzing the parallelogram of forces of muscle actions on a joint; a Hales cannulating the carotid artery of a horse, to mention but a few instances, show that these scientists stood in no awe nor impotence in the presence of life; and if they believed in vital force, which is extremely likely, they knew themselves to be in control of an experimental situation. In other words, they were reserving to science those things whereof science properly treats. In flogging vitalism, the author is beating a dead horse, but in substituting materialism he is attempting a veritable resurrection.

A concept that pervades the book may be illustrated by the following sentence: "We believe, that for every chemical process that takes place in a living cell—and there must be thousands of these—there is a separate system of enzymes." Now, first, nowhere is it made explicit that enzymes are to be regarded as catalysts—unless in the exuberance of latter-day enzymology this concept has been discarded. Second, the statement as it stands will not bear analysis. It leads to an infinite regression, for it would require enzymes to make enzymes . . . and the cell can only accommodate a few rounds of this. Although the author mentions physical chemistry, the *milieu interieur* of Claude Bernard, and the environment, there is no suggestion that they are really important in interpreting biochemical phenomena.

The Brain: Cells that Think, represents a phrase pregnant with unresolved promise. Cells do not think, either singly or collectively; tissue cultures do not think, nor do swarms of bacteria. Thought arises when cells have become infinitely interconnected by nerve processes, and then as a result of their interaction.

"We know of only one ubiquitous mechanism in living things—enzymes." This statement seems to fall into the category of what Whitehead has called the fallacy of misplaced concreteness. Here the author is badly in need of the services of one of the classical biologists he is going to discard in the final chapter—let us suggest D'Arcy Thompson. From the movements of ions to the construction of beehives there are ubiquitous mechanisms in life that are not enzymatic.

There is a remarkable attempt to show a difference between scientific and artistic genius. One passage seems so wrong-headed that it is worth quoting verbatim:

> In the field of science, genius accomplishes what lesser minds would accomplish later. Creation in the arts is quite different. It is inconceivable that anyone but Shakespeare or Beethoven might have brought forth those very same plays and symphonies. But Newton and Leibnitz independently and almost simultaneously integrated the same mathematical abstractions into differential calculus. The artist extracts his creation almost solely from the riches of his own mind; the scientist evolves in his mind a pattern from phenomena which he and others have pried out from observations of our physical universe. Genius among scientists can be measured in years—the number of years that he is ahead of his contemporaries.

It would take a book to demolish the half-truths and presumptions of these assertions. The author apparently denies the intuitive moment; the inspiration that comes from nowhere that a scientist would give his right arm to experience. Beveridge in his *Art of Scientific Investigation* surely comes nearer to both scientific dream and reality when he says, "In any event a great scientist must be regarded as a creative artist and it is quite false to think of the scientist as a man who merely follows the rules of logic and experiment." The assertion that a

dunce would eventually achieve what the genius discovered first runs counter to reason and history. During the selfsame thousand years that the Greeks moved from obscurity to the Acropolis, from ignorance to Aristotle, there were cultures that advanced from small mud huts to medium mud huts. One is forcibly reminded of J. Wesley Smith, the incomparable nincompoop who invariably misses the obvious; but how obvious is the still unknown? That great scientific generalizations necessarily or even frequently come out of accumulated data is untrue. Data followed, not preceded, the Theory of Relativity. The mighty generalization on the total energy of the Universe is not even confirmable by experiment—it can only be applied. Clerk Maxwell and Willard Gibbs most certainly extracted their creations from the riches of their own minds—and these creations are as individual as Macbeth or the Ninth Symphony of Beethoven. The scientific and artistic creations of Leonardo proceeded from the same mind, and one could add that Newton and Leibnitz just happened to be coincidental geniuses, a phenomenon not uncommon in the arts.

Throughout the book there appears to be a curious preoccupation with Nobel Prizemen. The layman may be forgiven for equating the Nobel Prize with a reward for genius. The scientist should know that it is an accolade, and not necessarily an imprimatur.

The final chapter, entitled A Credo, sets forth some articles of faith from which I, at least, beg leave to dissent. "Biology began as it will end—as applied chemistry and physics," states the author, quoting Hans Zinsser. "The classical biologist, or rather the biologist with the classical techniques for the study of life, is doomed eventually to technological unemployment," continues the author, on his own authority. Key sentences of the Credo appear to be the following: "A living cell is a patterned aggregate of ions and molecules—life is a sequence of interactions between these ions and molecules." Here the joker, invisible to the author, is the term "patterned," which is to say "organized." The biochemist had better decide what this means, as well as the implications of "sequence," before he discards the services of the "classical biologists," meaning, one supposes, the Darwins, Mendels, Helmholtzes, Sherringtons, L. J. Hendersons, and finally the Gowland Hopkinses.

This account of how a biochemist looks at life seems depressingly circumscribed, and the life it depicts is mechanistic and humdrum, and despite its industrious enzyme systems, is not going any place. It will be a pity if twentieth century biochemistry finds it necessary to fight the battles that nineteenth century physics fought and lost. When the author digresses from his task to make obiter dicta on Freud, St. Joan, DeNoüy, and the moral philosophy of Pasteur he smacks of scientific philistinism. To this, one may recommend in all charity, and great confidence, Hamlet, Act 1, Scene 5, line 165.

H. R. CATCHPOLE

FORTSCHRITTE DER CHEMIE ORGANISCHER NATURSTOFFE. *Volume Nine.*

Edited by L. Zechmeister. Authors: J. G. Baxter, H. Borsook, N. Bulman, D. H. Campbell, F. M. Dean, H. H. Inhoffen, H. M. Kalckar, W. S. McNutt, P. Meunier, H. Siemer, A. Stoll, and M. Tomita. Springer-Verlag, Wien. DM. 82.50 (cloth); DM. 79.00 (paper). xi + 535 pp.; ill. 1952.

The ninth volume of this series contains articles on carotenoid synthesis (Inhoffen), vitamin A synthesis (Baxter), ergot alkaloids (Stoll), Biscoclaurin alkaloids (Tomita), coumarins (Dean), and nucleosides and nucleotides (McNutt). While these reviews, written by outstanding experts, will interest chiefly the organic chemist, biologists will welcome a series of other articles dealing with antivitamins (Meunier), the biosynthesis of proteins (Borsook), enzymes of nucleoside metabolism (Kalckar), and the chemical nature of antigens and antibodies (Campbell). In the article on ergot alkaloids, novel cyclic structures formed by amino acids are described. In the article on protein biosynthesis, data of various laboratories on the incorporation of amino acids into proteins are recalculated and presented in comparable units. In the reviews of Borsook and of Campbell, biologists will find excellent presentations of the fascinating problems of protein biosynthesis and of antigen-antibody interaction.

F. HAUROWITZ



SYNTHETIC ORGANIC CHEMISTRY.

By Romeo B. Wagner and Harry D. Zook. John Wiley & Sons, New York; Chapman & Hall, London. $11.50. xii + 887 pp.; ill. 1953.

The book consists of a systematic collection of methods used in the preparation of mono- and di-functional organic compounds. In 39 chapters, each of them dealing with a definite group of organic substances, 576 methods are described. Each chapter is accompanied by tables listing the properties of the most important synthetic products, and by a list of references. Altogether, the book contains the amazing number of 6843 references. It will certainly be a very valuable reference source for organic chemists.

F. HAUROWITZ



ULTRAVIOLET SPECTRA OF AROMATIC COMPOUNDS.

By Robert A. Friedel and Milton Orchin. John Wiley & Sons, New York; Chapman & Hall, London. $10.00 (paper). vi + 52 pp. + 579 graphs. 1951.

The usefulness of this collection of UV spectra, which includes some 579 aromatic compounds, is obvious from the quantitative as well as the qualitative chemical point of view. In each case the spectral diagrams are accompanied by the common name of the compound,

the structural formula, and the solvent employed. The nomenclature follows in general that of *Chemical Abstracts*, but where differences occur, additional names are appended. References to outside literature are also included with each compound, although many of the spectra are presented here for the first sime. Two indices —of names and of formulae—will greatly assist the reader in the use of the volume. Introductory chapters, brief but sufficient for critical use of the contents, further add to a publication which should find much use in the hands of the chemist or biologist engaged in qualitative or quantitative identification of aromatic compounds.



ORGANIC REACTIONS. *Volume VII.*

Editorial Board, Roger Adams, Editor-in-Chief; A. H. Blatt, Arthur C. Cope, Frank C. McGrew, Carl Nieman, and Harold R. Snyder; Advisory Board, Louis F. Fieser and John R. Johnson; Associate Editors, James H. Brewster, Ernest L. Eliel, Howard A. Hageman, Walter H. Hartung, Marshall Kulka, Richard H. F. Manske, Ragini Phadke, Suresh Sethna, Robert Simonoff, Daniel Swern, and Oscar Touster; Former Members of the Board Now Deceased, Homer Adkins and Werner E. Bachmann. John Wiley & Sons, New York; Chapman & Hall, London. $9.00. viii + 440 pp.; ill. 1953.

This book is the seventh in the well-known series, *Organic Reactions*. With the publication of this volume, 66 reactions used commonly by organic chemists have been discussed and summarized. The current volume contains chapters on the Peckmann reaction, principally for the preparation of coumarins; the Skraup synthesis of quinolines; carbon-carbon alkylations with amines and ammonium salts; the von Braun cyanogen bromide method for cleavage of tertiary amines; the hydrogenolysis of benzyl groups attached to oxygen, nitrogen, or sulfur; the nitrosation of aliphatic carbon atoms; and the epoxidation and hydroxylation of ethylenic compounds with organic peracids.

The construction of the chapters has followed the plan of previous volumes. A general discussion which includes the scope and applications is followed by experimental directions and a tabulation of all of the substances prepared or reactions run up to the time the literature survey terminated. The experimental directions are not written for the novice but for the individual who has had some laboratory experience in synthetic organic chemistry.

C. E. KASLOW



MICROBIOLOGY

ANNUAL REVIEW OF MICROBIOLOGY. *Vol. VI.*

Edited by Charles E. Clifton. Annual Reviews, Stanford. $6.00. ix + 492 pp. 1952.

In a well-known annual publication such as this, naming the authors and giving the titles of the articles in full is of limited usefulness, particularly since this review will appear several months after the publication is generally available. In brief, the subjects covered are: the metabolism, nutrition, and genetics of microorganisms in general; soil microbiology; the classification and nomenclature of viruses; identification of viruses infecting plant tissue; bacterial viruses (bacteriophages); hemagglutination in relation to host cell-virus interaction; the influence of age on susceptibility to virus infections; the metabolism of spirochetes; human rickettsioses; associations between microorganisms and higher plants (mycorrhiza); nematodes parasitic on plants; toxoplasmosis; coryneform bacteria; the taxonomy of yeasts; antibiotics; standardization of immunological substances; antibodies; the mode of action of chemotherapeutic agents; and biological activities of metabolite analogs.

As usual, the quality of the individual reviews is high. The author index is extremely thorough, but the subject index is very weak (as in previous volumes). Also there is still no uniformity in the method of listing authors in the Literature Cited at the end of each review (see *Q.R.B.*, 26: 315. 1951). In 7 sets of references the authors are given alphabetically, but in the remaining 14 the authors are listed in the order in which they are mentioned in the text. This produces some scattering. In some sets of references the first and last pages of journal articles are given, in others only the first page. The former seems more desirable, in order to give an idea of the extent of the article.

WALTER C. TOBIE



BASIC BACTERIOLOGY. *Its Biological and Chemical Background.*

By Carl Lamanna and M. Frank Mallette. The Williams & Wilkins Company, Baltimore. $10.00. xiv + 677 pp.; ill. 1953.

This book will be welcomed by all those who hope that the teaching of bacteriology in American universities may ultimately become an intellectually respectable occupation. Lamanna and Mallette have attempted the very difficult task of writing an advanced textbook which presents bacteriology as an exact science. In so far as it deserves this appellation, bacteriology is a subject of great complexity. Its comprehension requires an extensive background in chemistry, physics, biology and mathematics, little of which can be taken for granted in the training of the average student. Hence if a textbook that is aimed at something more than the presentation of superficialities is to be a success, the bacteriological information which it conveys must be embedded in a large mass of scientific material drawn from other fields. Furthermore, the low critical standards which have prevailed in much of the bacteriological

literature make the selection of reliable data a formidable task. By imposing severe restrictions on the bacteriological subject-matter presented and taking up in detail the chemical, physical, and biological concepts which underlie this material, the authors have succeeded astonishingly well in coping with these difficulties. Comprehensiveness has of necessity been sacrificed. Only the unicellular true bacteria are treated, and many important phases of their biology—detailed descriptions of the special groups, parasitism and symbiosis, ecology of free-living forms—are largely or completely excluded.

Nearly half the book is concerned with the general physiology of eubacteria. This material comprises excellent chapters on the chemical and physical properties of the bacterial cell, the nature of the cell surface (which contains a valuable section on permeability), and the effect of physical factors on bacteria, growth, nutrition, and chemical disinfection. Bacterial metabolism occupies a single chapter 150 pages in length. The treatment is notable for a detailed description and evaluation of the various methods currently used in the study of intermediary metabolism. Non-physiological aspects of bacteriology receive much briefer treatment. They include a stimulating discussion of the general problems of bacterial taxonomy (30 pp.), a brief but adequate chapter on the essentials of bacterial genetics (35 pp.), and a chapter on the structure of the eubacterial cell (35 pp.), which is preceded by detailed accounts of microscopy and staining (75 pp.). The discussion of bacterial cytology is regrettably brief, and the illustrations are few and poorly chosen. This minor defect is particularly unfortunate, since no recent, scientifically acceptable survey of bacterial cytology is at present available.

A resume of its contents is insufficient to convey the special merit of this work: namely, its rigorous intellectual approach. The experimental bases of factual knowledge are clearly presented; hypotheses are scrupulously separated from facts, and critically evaluated; and areas of confusion or ignorance are indicated. A great many of the figures are reproductions of experimental data, and are accompanied by very detailed descriptions and interpretations. After the half-baked dogmatism, resting on shaky factual foundations, which characterizes so many bacteriological textbooks, it is singularly refreshing to encounter a book in which the intelligence of the reader is respected. In addition, the literary style is admirable. *Basic Bacteriology* can be recommended unhesitatingly to both students and teachers who wish to acquire a knowledge of the scientific foundations of bacteriology.

R. Y. Stanier



Symposium on Some Aspects of Microbial Metabolism. *Given at Research Conference for Biology and Medicine of the Atomic Energy Commission. Sponsored by The Biology Division, Oak Ridge National Laboratory, April 10, 11, 1952.*

Oak Ridge National Laboratory, Oak Ridge. Free upon request (paper). 282 pp.; ill. 1953.

This work is reprinted from the *J. cell. comp. Physiol.*, 41: Supplement 1, March 1953. Since it is essentially a super-reprint from a standard journal, rather than a separate publication, only a brief characterization is indicated.

The 13 papers deal with: the comparative biochemistry of microorganisms, respiratory cycles, structure of coenzyme A, enzymatic synthesis of acyl-coenzyme A compounds, the mechanism of the ATP-CoA-acetate reaction, the pyruvate oxidation factor (lipoic acid), metabolism of pentose phosphate, alternate pathways of hexose oxidation in *Pseudomonas fluorescens*, pentose and desoxypentose metabolism, routes of ethanol formation, propionic acid fermentation, biological functions of pteridine derivatives, and purine and pyrimidine metabolism. The papers are followed by discussions from the floor, and lists of references.

Despite its sponsorship, the symposium has little to do with atomic energy, except that "labelling" of compounds by the use of radioactive isotopes is occasionally mentioned. Nevertheless, as an account of recent advances in the topics mentioned, the publication has much of value and interest.

Walter C. Tobie



Tubercle Bacillus *and Laboratory Methods in Tuberculosis.*

By M. A. Soltys in collaboration with C. A. St. Hill and I. Ansell. The Williams & Wilkins Company, Baltimore. $4.50. vii + 212 pp. + 6 pls.; text ill. 1952.

This book is essentially an introduction to the study of the biological and chemical characteristics of the tubercle bacillus (human, bovine, and avian varieties), its isolation and identification, the chemotherapy of clinical treatment, and many related topics. There are many useful references, which seem well chosen from the thousands of contributions which have appeared on the subject. It can be highly recommended to those beginning a study of this organism, and should be useful for reference by those already engaged in the field.

It is regrettable that no mention is made, even in passing, of several strains of false "tubercle bacilli" (such as No. 607 of the American Type Culture Collection) which have been extensively used with misleading results for tests *in vitro*. Such cultures, mislabeled "*Mycobacterium tuberculosis*, avirulent fast-growing strain" and the like, have proven to be strains of the smegma bacillus in most cases. I know of at least one case where large sums were spent in searching for (and

finally finding) a synthetic drug active against No. 607, but which had no useful action against clinical tuberculosis.

This is of course a negative criticism, since a basic text cannot take in everything. Within its scope, the book should be of great value.

WALTER C. TOBIE



THE MICROBIOLOGICAL ASSAY OF THE VITAMIN B-COMPLEX AND AMINO ACIDS.

By E. C. Barton-Wright. Pitman Publishing Corporation, New York, Toronto and London. $4.00. x + 179 pp.; ill. 1952.

The widespread application of microbiological assays for the determination of substances of biological interest makes it necessary constantly to revise procedures in the light of improved technics. This volume describes newer methods of analysis for vitamins of the B-complex, except vitamin B_{12}, and for a number of the amino acids including leucine, isoleucine, valine, lysine, phenylalanine, histidine, serine, proline, glycine, arginine, threonine, aspartic acid, alanine, methionine, cystine, tyrosine, tryptophane, and glutamic acid. The assay methods described are those personally tested by the author and found to work satisfactorily. Helpful references are provided at the end of each section. In this respect, it seems to me that reference should have been made to the investigations of Novelli, Kaplan, and Lipmann on the enzymatic release of pantothenic acid from bound forms. A very useful chapter for the beginning student is on the assessment of the validity of microbiological assays and methods of computation.

R. VAN REEN



ANTIBIOTICS: A SURVEY OF THEIR PROPERTIES AND USES.

Published by direction of the Council of The Pharmaceutical Society of Great Britain. The Pharmaceutical Press, London. 25s. xii + 290 pp.; ill. 1952.

The first edition of this book published in 1946 (*Q.R.B.* 22: 360. 1947) has been brought up to date and includes details of commercial manufacture, chemistry, stability, methods of assay, and clinical application of the antibiotic drugs. Penicillin, streptomycin, chloramphenicol, aureomycin, and terramycin are considered.

C. JELLEFF CARR



PSYCHOLOGY AND ANIMAL BEHAVIOR

A TEXT-BOOK OF MENTAL DEFICIENCY (AMENTIA). *Eighth Edition. By A. F. Tredgold; assisted by R. F. Tredgold. The Williams & Wilkins Company, Baltimore.* $7.50. xvi + 545 pp. + 48 pl.; text ill. 1952.

This is the most recent edition of a classic text-book in the field of mental deficiency. The outline and material covered are similar to those of the 1947 edition. Additional references are made to recent studies on prenatal virus infections, toxoplasmosis, and maternal dietary deficiency as possible etiological factors in mental defect and congenital abnormality. The results of clinical experience with glutamic acid and thiamine are also discussed. The illustrations and chapters on the clinical varieties of mental deficiency are especially clear.

The section on "clinical examination" suggests test methods for determining mental status. It is unfortunate that this chapter was not rewritten to include developments in psychological testing and psychological practice in the excellent way that the chapters on pathology, etiology, and treatment were revised and brought up to date.

MYRTLE ASTRACHAN



HEALTH AND DISEASE

MANUAL OF THE INTERNATIONAL STATISTICAL CLASSIFICATION OF DISEASES, INJURIES, AND CAUSES OF DEATH. *Sixth Revision of the International Lists of Diseases and Causes of Death [Adopted 1948]. Volume 1. Bulletin of the World Health Organization. Supplement 1. World Health Organization, Geneva.* xxxvii + 376 pp. 1948.

The International Conference for the Sixth Revision of the International Lists of Diseases and Causes of Death which met in Paris in April, 1948, marked the beginning of a new era in international vital and health statistics. In addition to the adoption of a single comprehensive list of diseases, injuries, and causes of death, the Conference recommended the adoption of an extensive program of international cooperation in the field of vital and health statistics, and committed to the Expert Committee on Health Statistics of the World Health Organization the responsibility for establishing standard forms and procedures for the uniform medical certification of death and the analysis of death records throughout the world.

All vital statisticians agree that a standard classification of diseases and causes of death is essential for the statistical study of morbidity and mortality, and the present International List is certainly the best that has yet been devised. However, for those who are interested in the study of trends in morbidity or mortality, there are many disappointments in the new revision, because of the ever-recurring changes in classification and definition. For example, the changes have been such that in a comparison of cause-of-death assignments for 64

selected causes of death by the Sixth and Fifth Revisions of the International Lists for a 10 per cent sample of certificates filed in 1949 and 1950 in the State Vital Statistics Offices, the comparability ratios for several causes of death were as follows: syphilis and its sequelae, 0.74; diabetes mellitus, 0.57; anemias, 1.60; rheumatic fever, 2.67; hypertension without mention of heart, 6.54; and acute nephritis and nephritis with edema, including nephrosis, 1.79.

As if in anticipation of this criticism of the revised list, the authors have stated (Introduction, p. xxix): "The present classification represents an expansion of the disease rubrics of the previous International Lists to provide specific categories for nonfatal diseases and injuries. In this process of expansion, provision has been made so as to permit comparability of certain categories with important titles of the Fifth Revision of the International List. It is not essential, however, that there should be strict comparability for each individual subdivision. It must be remembered that when one compares the frequency of a disease or cause of death now and twenty years ago, one is not really comparing the actual frequency of that particular disease, but the frequency with which a particular term is used to describe a disease status by observers differing in their education and medical outlook by a period of twenty years."

It is distressing indeed to find that a task (the study of time trends), made difficult at best by uncontrollable gradual changes, should now be relegated to the realm of the impossible by the institution of controllable abrupt changes. Our only consolation is offered by Nietzsche: "Every step forward is made at the cost of mental and physical pain to someone."

B. AUBREY SCHNEIDER



PROCEEDINGS OF THE SECOND CLINICAL ACTH CONFERENCE. *Vol. I—Research. Vol. II—Therapeutics. Edited by John R. Mote. Blakiston Company, New York, Philadelphia, and Toronto.* $8.50 per vol. Vol. I: xxiv + 531 pp.; ill. Vol. II: xxiv + 716 pp.; ill. 1951.

The two volumes of this conference present an enormous amount of material of primary interest not only to clinicians, but also to all investigators into the complexities of the endocrines and their interrelations. The material covers everything from general adrenal cortical physiology to the effects of ACTH on practically all organs and systems.

The papers and discussions are clinical for the most part. It is a little difficult to see why one volume alone is entitled research, inasmuch as it does not appear to favor this aspect of the field any more than the other. The difference lies, perhaps, in that Volume II discusses *therapeutic research* in contrast to many of the papers in the first volume, which deal with more general or fundamental aspects of the problem.

It would also have been helpful to have some sort of index. Neither volume contains one. These proceedings will be most useful as a temporary reference work, but are presumably not expected to remain as a classic work in the field.

R. G. GRENELL



HORMONAL AND NEUROGENIC CARDIOVASCULAR DISORDERS. *Endocrine and Neuro-Endocrine Factors in Pathogenesis and Treatment. By Wilhelm Raab. The Williams & Wilkins Company, Baltimore.* $15.00. xxi + 722 pp.; ill. 1953.

This book formulates and elaborates a thesis that will be new to many, namely, that the complex neurohormonal control of the cardiovascular economy is an imperfect mechanism which provokes the heart and vessels to constant strain and predisposes them to serious disease. The action and potentiation of the catecholamines, epinephrine and nor-epinephrine, are basic in Raab's concepts. These substances, whether from adrenal medulla or nerve endings, produce myocardial hypoxia by increasing the myocardial oxygen demand out of proportion to any increase in work. There is even a narrow margin between the physiological and the lethal catecholamine concentration in the heart muscle. These substances may produce sudden changes, including fatal arrhythmia, or may predispose to arteriosclerosis and other degenerative diseases. Adrenal cortical steroids and the thyroid hormone potentiate the action of the catecholamines and are important in congestive heart failure and other pathological states.

Although controversial, the basic concepts are supported by much factual material. In all, 3726 references are cited. Nevertheless, the author admits that, in attempting to weld the parts into a cohesive clinical system and to crusade for the new ideas, he has been guilty of deliberately infringing upon the code of cautious understatement.

The book is divided into one basically experimental and two clinical parts, concerned respectively with endocrine and with cardiovascular syndromes. The endocrinological section is less valuable because it is repetitious and because it will be of interest primarily to those in endocrine fields who are already familiar with the material. Despite repetitions and overdevelopment, the book is a scholarly and readable presentation. It should prove informative and stimulating to readers on both a theoretical and practical level.

E. CONVERSE PEIRCE, 2ND



INTERNATIONAL JOURNAL OF GROUP PSYCHOTHERAPY, *Vol. I, No. 1, April 1951.*

Official Publication of The American Group Psychotherapy Association (formerly The American Group Therapy Association).
Editorial Committee: Samuel B. Hadden (Chairman), Nathaniel J. Breckir, Helen R. Durkin, Charles G. McCormick, Harris B. Peck, S. R. Slavson, and Hyman A. Spotnitz. Consulting Editor: S. R. Slavson. Assistant Editor: Lottie M. Maury. International Universities Press, New York. Annual subscription: $7.50; single issues: $2.00. No. 1: 92 pp. 1951.

This is the first issue of a new psychotherapeutic journal which is to appear six times a year, and to deal with "group" problems of sociological, psychological, and therapeutic nature. In addition to original contributions, each issue will include book reviews and abstracts related to the specific subject the journal is fostering.

Without wishing to question the interest of papers devoted to group work for those in this field, one is worried (as others have been, more and more frequently in recent years) about what the future will be if each new group of workers concerned with some specific idea within a field finds it necessary to have their own journal.

R. G. GRENELL



HUMAN BIOLOGY

SOCIAL EVOLUTION.
By V. Gordon Childe. Henry Schuman, New York. $3.00. viii + 184 pp. 1951.

The data of archeology have never been integrated. Each archeologist is a specialist working within the more or less narrow limits of his own field. From time to time it may be possible to fit together a few contributions from different investigators, like the pieces of a jigsaw puzzle, but the general picture still eludes us.

It is widely considered that the human species in its cultural development has passed through three successive stages—savagery, barbarism, and civilization—but there is no unanimity regarding the events which mark the boundaries separating them. Some would say that civilization began with the invention of writing, others, with the invention of the plough, still others with the acquisition of the technique for working iron, and so on.

The difficulty arises from the fact that the skills to use these devices are not always acquired in the same order. The Mayas, who had invented a vigesimal numerical system with a symbol for zero several centuries before Leonardo of Pisa introduced the Arabic numerals into Europe, and who possessed a well developed system of writing, had no domestic animals and no knowledge of the plough. Their agriculture was that of the hoe, the art of using which they had learned presumably from the inhabitants of the Peruvian altiplano, who possessed herds of domestic animals and had developed maize to the point where it was fit for human consumption, but who remained quite illiterate. Apparently the arts concerned with the satisfaction of the primary needs of food, clothing, and shelter diffuse more rapidly than those whose effect is largely cultural.

The conclusion at which the author finally arrives is that civilization began with the invention of the city—a population of specialists who depend upon each other for all the prerequisites of their standard of living, and who therefore had to learn to cooperate with each other. It is clear that people who lead a nomadic existence, or who cultivate large tracts of land, might acquire the ability to make tools, but it is not likely that they would make more than sufficient to satisfy their own needs; the farmer who made bronze hoes used them himself, and the fisherman who made fish-hooks from the same material also used them himself; neither one made tools for the other. In order for smithery to be developed as a separate vocation, it was necessary that a system of living should be developed in which followers of different occupations could rub shoulders one with another, a way of life possible only in the city. Generally speaking, the city came into being when men discovered the secret of working with iron, but there are some exceptions. Some nomadic peoples of the Old World knew how to work iron, but none of the dwellers in the pre-Columbian cities of the New World used iron tools. However, we do not know exactly to what extent city life was developed in America prior to the arrival of the conquistadores. The Peruvians left no record; those of the Mexicans went up in the smoke of the holocaust of Bishop Lando. The so-called cities of pre-historic America may have been merely over-developed haciendas in which the numerically largest demographic element was that of the slaves ruled by an imperialistic minority, in which cooperation was completely precluded.

Cities tend to develop personalities that distinguish them from other cities. The author cites no examples, but we all know, for instance, what a large role the valleys of the Mohawk and Hudson rivers have played in making New York the financial capital of the United States, and how the growth of Chicago has been made possible by the wheat fields of the northwest. The coal and iron mines of Pennsylvania have made Pittsburgh the center of the national steel industry; though it is somewhat difficult to account for the concentration of manufacturers of automobiles in Detroit or of saxophones in Elkhart, Indiana. Yet all of these cities have more in common with each other than with the rural areas which surround them. They are occupied by workers who use personally only a small portion of the goods which they produce. These become cooperating specialists and cease to be competing individualists, at least in idealistic theory.

A large portion of *Social Evolution* is devoted to a discussion of the difference between organic and cultural evolution. The former begins with an advantageous

mutation, and a struggle for survival in which those individuals which lack the mutation are eliminated. Social evolution also begins with an advantageous mutation, but the struggle for survival is not inevitable; the mutation spreads not by inheritance but by diffusion. Two natural results follow, first, social evolution takes place with greater rapidity than does organic evolution, and second, social or cultural evolution may be convergent as well as divergent. If two widely different cultures come into contact, each may adopt some traits characteristic of the other, so that the differences between them may be obliterated and the two coalesce. And thus the fact noted at the beginning of this review, that developing cultures do not always pass through homologous stages in the same order, can be explained. The order in which successive cultural stages are entered is determined by the order in which contact with other developing cultures is made.

It is to be hoped that this small book will receive such an enthusiastic reception that the author will be encouraged to write a longer one covering the same field in greater detail.



THE FOUR AGES OF TSURAI. *A Documentary History of the Indian Village on Trinidad Bay.* *By Robert F. Heizer and John E. Mills; translations of Spanish documents by Donald C. Cutter. University of California Press.* $3.75. x + 207 pp.; ill. 1952.

Tsurai is the name of a former Indian village, located on Trinidad Bay, which became extinct at about the turn of the century. The four ages are respectively those of the Indians before discovery by the Europeans, the period of discovery and exploration, the period of exploitation due to the development of the fur-trapping industry, and the period of settlement and colonization after the admission of California to statehood.

With the exception of the opening chapter, in which the results of archeological investigation of the site of the village are reported and discussed, the book consists almost exclusively of excerpts from original documents; about half of these were originally in Spanish, but are presented here in English translation. The intention of the editors has been to integrate and make accessible what is known about the cultural life of the Yurok Indians, and the documents have been carefully selected with this end in view.

Noticeable is the peculiar hiatus between the years in which Mexican rule began and ended. The editors explain that they were unable to find any documents dealing with this interval, and question whether any vessels put in at Tsurai during those years. A simpler explanation seems more reasonable. From 1811 to 1844 the fur trade of the western North American coast was monopolized by the Russians, who maintained headquarters at Fort Ross. During this interval there was considerable maritime traffic between this point and the ports of Alaska and Kamchatka. It is inconceivable that none of those expeditions stopped at Trinidad Bay to pick up hides and furs. It is more likely that reports of them are on file behind the Iron Curtain where they are not accessible to Western historians. Such documents might not add a great deal to our knowledge of Yurok culture, but they would throw light on the personalities of those who participated in the expeditions.

On the whole the most striking contribution of this book is not what it tells us about the Yuroks, but what it tells us about the white people who visited these shores. The Spaniards and the Anglo-Americans came from widely differing cultural backgrounds, but they were both activated by the same motive, greed. Both made slaves of the braves and harlots of the squaws. On the other hand, the two documents from German sources seem to indicate that their writers were motivated only by a thirst for knowledge, and that they considered the Indians to be their social equals. This recalls the fact that in all the Atlantic Coast colonies, except one, interracial friction was continually developing; the freedom from such in Pennsylvania is generally credited to the Quakers. May not the fact that the frontier in Pennsylvania was so largely settled by Germans be in some degree responsible for the three quarter centuries of peace enjoyed by this colony? Such speculations are interesting.



HOW TO SURVIVE ON LAND AND SEA. *Individual Survival. The Naval Aviation Physical Training Manuals. Revised Edition prepared by The V-Five Association of America; First Edition prepared by Officers of the Aviation Training Division, Office of The Chief of Naval Operations, U. S. Navy. United States Naval Institute, Annapolis.* $4.00. xviii + 340 pp. + 1 folded map + 1 folded chart; ill. 1951.

Although serious in purpose, this book might well have been prepared as an answer to that perennial question about the best book to be shipwrecked with. In some ways, it is an improvement over the Boy Scout Handbook for the purpose, but it is not as compact. However, this is actually the text for an intensive course in survival for downed airmen, originally assembled in 1943 to meet the urgent needs of war; it has been issued in this revised version for more general use. It includes not only the usual woodcraft and beachcombing techniques, but is also a sort of practical ecology, accompanied by a large folded chart of world types of vegetation.

JOEL W. HEDGPETH



DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

A POPULAR GUIDE TO GOVERNMENT PUBLICATIONS. *By W. Philip Leidy. Columbia University Press, New York.* $3.00. xxii + 296 pp. 1953.

During the years 1940 to 1950, the Government Printing Office in Washington, D. C. turned out over 200,000 different publications. Although the majority of these technical publications of various sorts, a large number of them are of interest to the ordinary citizen. Leidy has done the public a service by poring over the mass of titles, weeding out the technical items, and retaining a list of 2,500 titles likely to have popular appeal. The titles in the book are arranged by subject, and indexed. A brief description of each is provided unless the title is self-explanatory, and information is given on how to obtain each one. An invaluable book for those wishing to take advantage of the government information services, it may also be expected to stimulate the sale of the particular publications included. In view of the rapidity with which the availability of Government publications changes, it is to be hoped that the book will be revised frequently. The present list holds titles that should be of great interest to school libraries, librarians, vocational guidance counselors, teachers, students, campers housewives, amateur or professional gardeners, farmers, carpenters, mechanics; anyone with a hobby, and probably everyone.

A. T. JAGENDORF



CLINICAL LABORATORY METHODS. *Fourth Edition. By W. E. Bray. The C. V. Mosby Company, St. Louis.* $7.25. 614 pp. + 18 pl.; text ill. 1951.

The present text appears to be intended both for medical students and for medical laboratory technicians. It is excellently and abundantly illustrated and contains a large amount of highly condensed material on urinalysis, hematology, blood chemistry, gastric analysis, feces and intestinal parasites, sputum, cerebrospinal fluid, bacteriology, mycology, water and milk, serology, basal metabolism, allergies, poisons, drug assays, surgical pathology, and other topics. Much new material has been added since the third edition (1944). There are many useful references in the text and in footnotes. The work appears to have gained wide acceptance, if the four reprintings of the Third Edition are any indication.

A few minor deficiencies are apparent. Since the book is printed exclusively on glazed paper (owing to the many illustrations), it is rather heavy to handle. In the review copy, the quality of the text varied from very light to very heavy printing. Nevertheless, the book merits careful examination by those giving instruction in the subjects mentioned above.

WALTER C. TOBIE



PHILOSOPHICAL PROBLEMS OF MATHEMATICS. *By Dr. Bruno Baron von Freytag gen. Löringhoff; translated from the German by Amethe Countess von Zeppelin. Philosophical Library, New York.* $2.75. viii + 88 pp. 1951.

The author of this work is a brave and bold man who does not mind "sticking his neck out." His fundamental premise is that all the natural sciences, and mathematics as well, have problems of fundamental importance that cannot be solved by the methods of science, and frequently cannot even be expressed in the language of science, because that language is too precise. It is difficult to imagine a mathematical problem soluble only by a technique that lies outside Karl Pearson's definition of scientific method. (Pearson, incidentally, was both mathematician and philosopher, yet his name is not mentioned in this treatise.) One would think that a procedure capable of solving a mathematical problem would by virtue of that very fact be a mathematical procedure. The author thinks not, and believes that recourse must be had to philosophy. As example, he cites the theory of probability as an instance of the applicability of philosophic method to a mathematical problem. To me the theory of probability has always seemed just the opposite—an application of mathematical technique to a philosophical problem.

Perhaps a better illustration would have been the axioms of mathematics. Are these axioms true? They were certainly considered so as long as no system of mathematics other than that of Euclid was known. But we know now that systems of mathematics can be erected on sets of axioms inconsistent with those postulated by Euclid. Here the author draws a distinction between Reality and Truth. Reality is what we apprehend empirically; Truth is what we apprehend by a process of ratiocination. Are the objects of mathematics apprehended by the one method or the other? or by both? E.g., is a triangle real or true? Certainly we can visualize a triangle, and we can learn facts about it by the application of mathematical logic. We experience objects that we believe to be triangular, and therefore we conclude that triangles have a real existence. But what can we say about an imaginary triangle, the sum of whose angles is not equal to two right angles? We cannot visualize such triangles and we do not encounter them in nature, but by applying the same mathematical logic to them we can learn what the world would be like if such triangles did exist. Therefore the triangles, though not real, are true, and the mathematical system based upon belief in them is good. Such triangles cannot exist in the mathematics of Euclid, but they can and do exist in the mathematics of Riemann. This is what Korzybski meant by saying that an object could be both existent and nonexistent, and for this reason he rejected the logic of Aristotle. The author of the present work would express the same thought more lucidly (and I think more accurately as well) by saying that such a triangle is true but not real.

The book is very difficult reading. The following quotation is a sample of the way in which the authors' literary style appears in translation.

"It would be a hopeless task to attempt to force a close union of the domains of (concrete) Reality and of mathematics which are logically incompatible structures, if there did not exist, even in the contradictory systems of (concrete) Reality a principle of identity which is shared by both mathematics and logic. We discover this identity expressed, for the most part, in two different forms: in the one, every space-time structure, every point, every line, every solid, every hypersolid, of this four-dimensional space-time manifold, is in the strictest logical sense identical with itself; and in the other, every one of these structures has the whole-part relation to both its finite and infinitesimal 'parts.' These 'parts' by virtue of being components of identically the same structure are united in an identity of a higher and more complex kind which in the special case of the individual in time, we denote as 'genidentity.'"

The author assumes a much greater knowledge of the contemporary writers in related fields than many readers will possess. There are many references to such writers in the footnotes. The influence of this book would have been augmented had the philosophies of these contemporary writers been expounded in the text. This would of course have expanded the treatise to several times its present size, which would nonetheless have been an improvement.

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Material ordinarily taking the form of footnotes is set in small print and placed in the text and consequently should be written in a style so as to fit readily into the text. Acknowledgments are printed in the text in small type at the end of the article just preceding the List of Literature. Recent issues of the Quarterly should be examined for style as regards (1) section or subsection headings in the text, (2) literature citations in the text, and (3) List of Literature.

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